A REVISION OF THE NORTH AMERICAN SPECIES OF THE
CICINDELA MARITIMA GROUP WITH A STUDY OF HYBRIDIZATION BETWEEN
CICINDELA DUODECIMGUTTATA AND *OREGONA*

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The North American species of the Cicindela maritima *group are:* C. duodecimguttata *Dejean;* C. oregona *LeConte;* C. depressula *Casey;* C. repanda *Dejean;* C. hirticollis *Say;* C. limbata *Say;* C. columbica *Hatch;* C. bellissima *Leng; and* C. theatina *Rotger. The male genitalia of these species are described. The group is diagnosed and two keys are given, one based on non-genitalic characters, and the other based on features of the male genitalia. For each of the species* duodecimguttata, oregona, *and* depressula *the following are presented: synonymy, analysis of geographic variation in size, coloration, color pattern of elytra, and distribution. Descriptions of the subspecies of* oregona *and* depressula *are given. Hybridization between the species* duodecimguttata *and* oregona *is examined quantitatively by means of the hybrid index method and the data are presented in the form of histograms. The zone of hybridization lies on the eastern slopes of the Rocky Mountain System from Colorado to the Northwest Territories, and is about 50 miles wide in Alberta but is nearly 1,000 miles wide in northern Canada. Variation of external characters and shape of the median lobe of the male is greater in the region of intergradation than it is within the range of the pure parental forms. Temporal variation occurs in hybrid populations. Phylogenetic and zoogeographic relationships are postulated to explain the structural similarities and distribution patterns of the North American species of the* maritima *group.*

INTRODUCTION

The species of the North American tiger beetles of the genus *Cicindela* are for the most part fairly well understood taxonomically, and it is possible to identify most adult specimens as a result of publications by Leng (1902), Horn (1915), Cazier (1936, 1948, 1954, 1960), and Wallis (1961). In addition Hamilton (1925) has described many larvae. With the descriptive phase in this condition attention must now be directed to taxonomic studies at the species level. By such studies phylogenetic relationships of species and delimitations of species groups within the genus can be worked out.

This study began with the discovery of hybridization between *Cicindela duodecimguttata* and *Cicindela oregona*. Variation of phenotypic characters of hybrids and pure parental forms was analysed. As a result it was found that the latest definition of *oregona* (Wallis, 1961) was composite and included the definition of *depressula*. This led to a study of *depressula*. The male genitalia of all the North American species of the *maritima* group were then examined. The features of the internal sac proved to be diagnostic of this group, while shapes of the median lobes were found to be specifically distinct.

MATERIALS AND METHODS

Materials

Structural features and their variation were studied in approximately 12,000 specimens of *C. duodecimguttata*, *C. oregona* and *C. depressula*. The data from these observations are analysed quantitatively by the following techniques. Descriptions and specimens of larvae of seven species were also examined but only as additional material for deriving a phylogenetic scheme for the North American species of the *maritima* group.

Methods

External Characters

Distribution of hairs on the head, elytral pattern, and color are very important in the classification of the North American species in the *maritima* group.

Hairs may cover the head and frons either very densely or sparsely, or they occur in the form of a patch near the inner edge of each eye. The post genae may be glabrous or hairy.

Elytral pattern is composed of the following white markings: humeral lunule, marginal band, middle band, and apical lunule. The occurrence, shape, and expanse of these markings are used in showing interspecific and intraspecific variation (figs 11-16).

The six basic colors that occur in *duodecimguttata*, *oregona* and *depressula* were matched with the color standards of Ridgway (1912). They are listed below with their corresponding Ridgway names in parentheses: black (Black), brown (Mummy Brown), copper (Liver Brown), purple (Dull Violet Black), blue (Dusky Green Blue), and green (Danube Green). These colors may be dull, opalescent, or metallic.

Male Genitalia

North American species of the *C. maritima* group can be grouped together and individually identified by characteristics of the male genitalia. For study of the genitalia the male beetle was relaxed in boiling water. Then by inserting a pair of fine forceps into the end of the abdomen the genitalia were grasped and pulled out. These structures were cleared in a hot 10% solution of potassium hydroxide for about 10 minutes and then washed in water. The genital structures were finally stored in glycerine in a corked microvial and pinned beneath the beetle from which they were extracted. Drawings of the male armature were made with the aid of a Wild camera lucida and stereoscopic microscope at a magnification of X 62.5.

Measurements

Intraspecific variation of size and expanse of color pattern was

analysed by means of measurements. A calibrated eyepiece in a Zeiss stereoscopic microscope at a magnification of X 10 was used. Relative size is indicated by length of elytra as measured from the apex of the scutellum to the tip of the elytral spine and width of the elytra as measured from the midline to the margin at the widest point. Expanse of elytral pattern is represented by the transverse diameter of the apical dot. Measurements were made of specimens in each large population sample.

Statistical Methods

Linear measurements were treated statistically and tabulated. The range, mean, standard deviation, coefficient of variation, and standard error, were determined in each analysis. The Chi-square test was used in evaluating data of annual and seasonal changes in hybrid indices of population samples. The method was also employed to assess randomness of mating in the hybrid zone (Simpson *et al.* 1960, p. 306).

Hybrid Index

Variation in a hybrid population can be analysed using a hybrid index. This method was developed by Anderson (1949) for plant hybrids and has been successfully used for study of variation in avian hybrid populations (Sibley 1950, 1954, Sibley & Short 1959a, 1959b, 1964, Short 1963). The hybrid index method makes it possible to describe variation in quantitative terms. The hybrid index is constructed as follows. Characters that separate the parental forms are determined. Each character of one parent is scored 0. Those of the other pure parent are each given a high value and intermediate characters are ascribed values that fall on the scale between the parental scores. The hybrid index for each specimen is the sum of its individual character values.

The method was used to analyse variation in *duodecimguttata - oregona* hybrid population samples. Results are presented in figures 35 to 44. In addition, geographic variation in elytral pattern of *duodecimguttata* is analysed by this technique (table 3). Because of its broader application the hybrid index is here also referred to as the "compound character index". In figs 35 to 43 average index changes per mile are indicated between localities of population samples. These roughly illustrate relative spatial rates of index change, but they do not imply linear trends.

Pictorialized Scatter Diagrams

Pictorialized scatter diagrams, the alignment of symbols in a two-dimensional field or graph, are used to describe several character relationships. The positions of symbols are determined by the calibrated axes each of which is a quantitative expression of a single character or ratio of two characters. More characters can be considered at a time by adding appropriate tokens to the specimen symbol. This method is used to illustrate data on intraspecific relationships of *oregona* populations (figs 22 - 31). For a more complete description of this method see Anderson (1949).

Pie-graph Maps

This method illustrates geographic relationships of populations with different varying color characters. Pies plotted on a map represent geographic positions from which population samples were collected. Numbers of specimens of particular color combinations are indicated opposite the appropriate pie sections (figs 19, 20).

Field Methods

Because tiger beetles are rather difficult to see in their natural environment a technique was necessary to facilitate field observations. At Nordegg, Alberta, in the hybrid zone, specimens were first caught with an insect net. The sex and hybrid index value of each individual was translated into a code that was painted on the elytra with a small brush. The individuals were then released and observed through field glasses.

Adult tiger beetles, collected for museum material, were killed in a jar containing potassium cyanide, and pinned the day they were caught.

Larvae were either trapped at the tops of their burrows by rapidly driving a shovel beneath them, or dug out. They were boiled in water five minutes to preserve their color and then placed in 70% alcohol.

Criteria for Species and Subspecies

Two similar forms are regarded as distinct species if their geographical ranges overlap and if they show no intergradation in at least one character (color excluded). If a narrow stabilized hybrid belt is developed in the region of contact of two forms that are largely allopatric they are treated as distinct species (Mayr 1963). Two allopatric forms that differ only in coloration are judged to be conspecific. Allopatric forms of a single species are regarded as being subspecifically distinct if 75 per cent of the individuals of one form are different from 97 per cent of the individuals of the other (Mayr *et al* 1953). However, if a clinal series of intermediate populations is intercalated between two distinct populations that are widely allopatric subspecific names are not given.

There are two opposing views regarding the subspecies concept. Wilson and Brown (1953) believe the subspecies concept to be subjective and arbitrary in the light of discordant variation, variation in microgeographic races, and the artificiality of quantitative methods of defining the formal lower limits of the subspecies as well as other reasons. Inger (1961) however, argues that Wilson and Brown tend to magnify exceptional cases, and that the subspecies concept despite its limitations has proved useful. It is this latter view that is followed in this text. Many more opinions regarding the subspecies concept are expressed in issues of Systematic Zoology (1953-1960).

MORPHOLOGY OF THE MALE GENITALIA OF THE NORTH AMERICAN SPECIES OF THE *CICINDELA MARITIMA* GROUP

Introduction

Several papers dealing wholly or in part with the male genitalia of American tiger beetles have been published (Horn 1930, Papp 1952, Rivalier 1954, and Rumpp 1957). Horn observes that for some races of *Omus californicus* Eschscholtz shape and size of the penis is characteristic. Papp presents a detailed study of the internal sac from which relationships of the Nearctic and Palearctic tiger beetles are deduced, while Rivalier classifies the entire *Cicindela* fauna of the Americas. Rumpp uses male genitalia in separating more clearly the species *Cicindela praetextata* LeConte and *Cicindela californica* Menetries.

Male genitalia of three or more specimens of each North American species of the *maritima* group were examined. The male armature consists of three relatively large sclerites: a median structure called the median lobe, penis, or aedoeagus (see fig. 1); and a pair of lateral parameres, one on each side of the median lobe and articulating with its base. Inverted in the median lobe is the membranous internal sac that is everted from the dorso-apical portion of the median lobe during copulation.

Within each species the shape of the median lobe is quite uniform. There is, however, a considerable amount of interspecific variation, particularly in form of the apex, that proves useful in distinguishing species of the *maritima* group from one another.

The internal sac comprises many folds, dark areas bearing microtrichia or aculeae, and sclerites. These fields of aculeae, and sclerites can be homologized within the species of the *maritima* group. Numbers are assigned to sclerites and letters are assigned to fields. This system of nomenclature follows that of Ball (MS) and is not synonymous with that of Papp.

When retracted in the abdomen the median lobe lies lengthwise, parallel to the longitudinal plane of the body of the beetle, and the opening of the internal sac is dorsal. When the median lobe is in a copulatory position the aperture of the internal sac is ventral. For each species drawings of the retracted median lobe and the inverted internal sac viewed from the dorsal and left sides are presented. In addition the shape of the apex of the median lobe is given separately for each species. Included also is a table of the various sclerites of the internal sac for each North American member of the *maritima* group.

Descriptions

Male Genitalia of Cicindela duodecimguttata Dejean

The median lobe is of average breadth and length (figs 1a, b, c, and 10). Two broad, lateral flanges that occupy the apical region of the median lobe converge apically to form a marked tip which curves

ventrally.

     The inverted internal sac, in which three fields of aculeae are distinct is clearly visible. These darkened areas are labelled a, b, and c. Field *a*, which has a pebbly appearance is apical in the infolded position but it is basal when the internal sac is everted. Field *b*, ventral in position, is a finger-like projection of the membrane from which only the apical end is separate in the form of a tiny sac. When the internal sac is inverted *b* hangs inward whith its free end nearest the apex of the median lobe. Conversely, when the internal sac is everted, this field projects outward its blind end remaining oriented toward the apex of the median lobe. Field *c*, is three quarters circular, anterior in the infolded position, and appears to serve as the apical limits of the everted internal sac.

     Six sclerotized areas are present. Most noticeable is the flagellum (4) which is a slender strip, pointed apically, and widened and hooked at the base. A short rectangular sclerite (3) is present to the left of the base of the flagellum, and sclerite 5, a cuplike structure, lies posterior to 3. In fig. 1 sclerite 5 lies to the right of the median line beneath several membranous folds, but it is more clearly shown in fig. 2. To the left of and lying in part over the basal portion of the flagellum is sclerite 1, a quadrate plate. Sclerite 6 is oriented to the right of the sagittal plane. It is twisted basally and resembles an aculeate field apically. Sclerite 2 is an elongate curved strip with its apical end near that of the flagellum. A very small triangular sclerite is present between 2 and 6, but it is not numbered since it may be a disconnected piece of one of these two sclerites. This sclerite is illustrated with sclerite 2 in fig. 10.

Male Genitalia of Cicindela oregona LeConte

     Shape of the median lobe (figs 2a, b, c, and 10) is quite different from that of the preceding species. Though the apical, lateral flanges are about as long as those of *duodecimguttata* they are rather narrow. The apex is not markedly curved ventrally. Fields and sclerites, excepting sclerite 5 which is relatively large, look like their counterparts of *duodecimguttata*.

Male Genitalia of Cicindela depressula Casey

     Unlike the penes of *duodecimguttata* and *oregona* the apical portion of the median lobe in this species is characterized by wide lateral flanges that form a blunt tip (figs 3a, b, c, and 10). The flanges are continuous and not separated from one another by the raised apical section of the chamber containing the internal sac as they are in the two preceding species. The median lobe is short and broad. Field *a* is composed of several elongate folds that together form a rough area. Field *b* is comparatively light, and *c* is c-shaped. Sclerites 1, 2, 3, 4, and 6 are respectively of the shapes and in the positions described for those of *duodecimguttata*. At the basal end of sclerite 2 the small triangular sclerite is elongate. Sclerite 5, large and lightly sclerotized, is visible when the internal sac is everted or inverted.
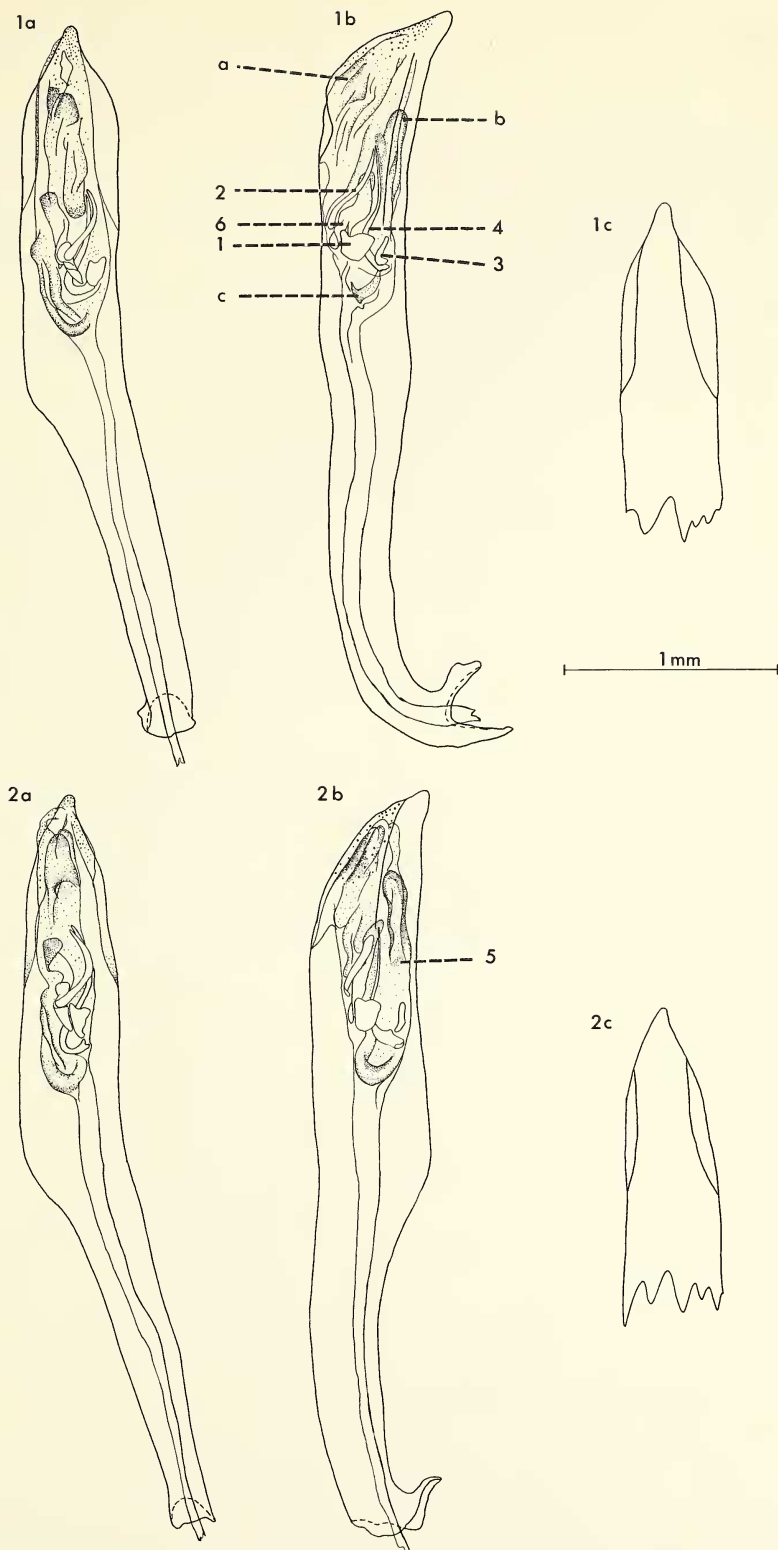
Fig. 1. Median lobe and inverted internal sac of *Cicindela duodecimguttata.* 1a, dorsal aspect; 1b, left lateral aspect; 1c, apical portion, dorsal aspect. Numbers = sclerite nos. Lower case letters = fields.

Fig. 2. Median lobe and inverted internal sac of *Cicindela oregona.* 2a, dorsal aspect; 2b, left lateral aspect; 2c, apical portion, dorsal aspect.

Male Genitalia of Cicindela repanda Dejean

The portion of the median lobe that contains the internal sac is more apically confined than those of the three discussed species (figs 4a, b, c, and 10). The lateral flanges are narrow and widely separated dorsally by the chamber of the internal sac. Field *a* is small and lightly aculeate, while *b* is a distinct area pebbly in appearance. Field *c* is of the common shape. Sclerite 1 is large and triangular, while 2, 3, 4, and 6 are like those of *duodecimguttata*. There is no small sclerite near the basal end of 2. Sclerite 5, large and heavily sclerotized, is quite distinct.

Male Genitalia of Cicindela limbata Say

The median lobe is relatively short and narrow (figs 5a, b, c, and 10). The two broad, lateral flanges are evenly rounded and together converge to a marked but non-protruding apex. Fields *a* and *b* are strongly aculeate; and *c* is clearly indicated in the form of one third of a circle. Variation is evident in the shape of sclerite 1 which is generally smaller in size than those of the other North American species of the *maritima* group. Sclerites 2, 3, 4, and 6 are of the common shape, and sclerite 5 is absent.

Genitalia of Cicindela bellissima Leng

The median lobe is of average length but thicker than those of the preceding species (figs 6a, b, c, and 10). From a dorsal view the lateral flanges compose a broad apical region that terminates as a sharp projecting tip. Field *a* is clearly indicated by its dark compact appearance. Both *a* and *b* have large and scale-like aculeae. Field *c* is three quarters of a circle. Sclerites 1, 2, 3, 4, and 6 are each of the common shade intensity and shape. Sclerite 5 is absent.

Male Genitalia of Cicindela columbica Hatch

The median lobe is relatively long and slender (figs 7a, b, c, and 10), the apical region comprises two fairly wide lateral flanges that are slightly constricted basally, and an unprojected, rounded apex. Prominent aculeae occur on field *a*, which is smaller and less compact than that of *bellissima*. Field *b* is a lightly shaded area, while *c* is of the common type. Sclerites 1, 2, 3, 4, and 6 each resemble their counterparts in other species of the *maritima* group. The sclerite between 2 and 6 is large and heavily sclerotized. Sclerite 5 is small and field-like in appearance which makes it difficult to detect.

Male Genitalia of Cicindela hirticollis Say

The median lobe is elongate and thick (figs 8a, b, c, and 10). The chamber which contains the internal sac is extended dorso-apically so that the lateral flanges are widely separated, and the apical portion of the median lobe is obscured when viewed from the dorsal side. Field *a* is composed of several elongate folds; *b* is sparsely aculeate;
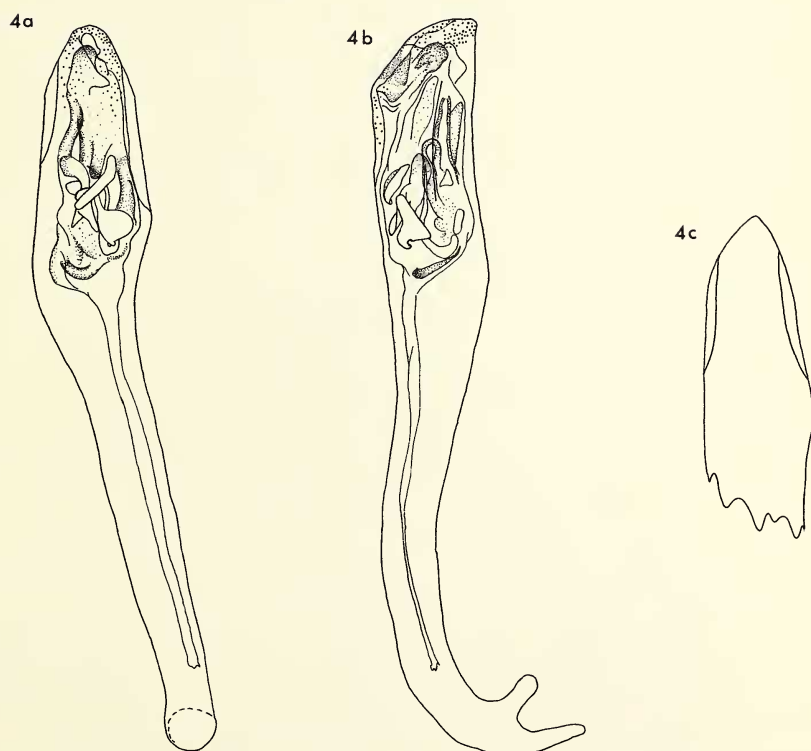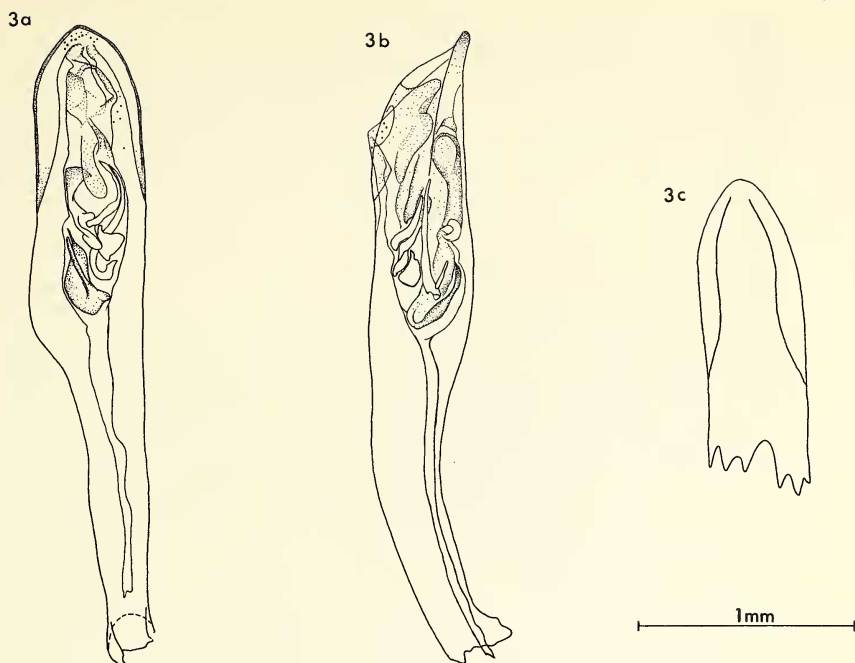
Fig. 3. Median lobe and inverted internal sac of *Cicindela depressula*. 3a, dorsal aspect; 3b, left lateral aspect; 3c, apical portion, dorsal aspect.

Fig. 4. Median lobe and inverted internal sac of *Cicindela repanda*. 4a, dorsal aspect; 4b, left lateral aspect; 4c, apical portion, dorsal aspect.
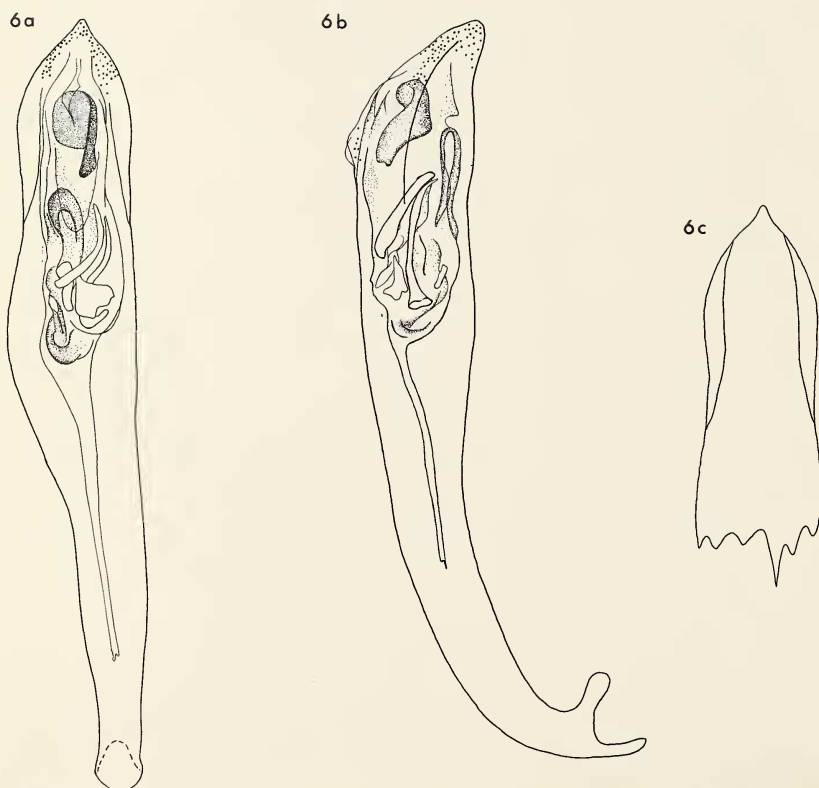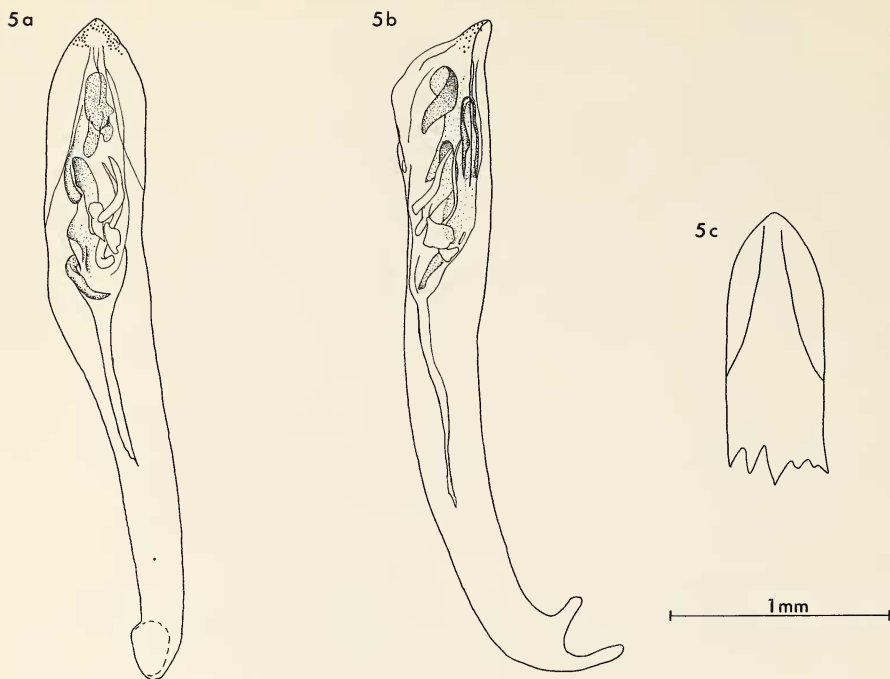
Fig. 5. Median lobe and inverted internal sac of *Cicindela limbata*. 5a, dorsal aspect; 5b, left lateral aspect; 5c, apical portion, dorsal aspect.

Fig. 6. Median lobe and inverted internal sac of *Cicindela bellissima*. 6a, dorsal aspect; 6b, left lateral aspect; 6c, apical portion, dorsal aspect.

and *c* is a semicircle. Sclerite 1 is relatively lightly sclerotized. Sclerites 2, 3, and 6 each have the shape characteristic of the *maritima* group. The sclerite between 2 and 6 is large and rectangular much like that of *columbica*. The apical twirl in sclerite 4 is markedly pronounced. Sclerite 5 is broad and lightly sclerotized.

Male Genitalia of Cicindela theatina Rotger

The median lobe is of average length and breadth (figs 9a, b, c, and 10), the apical region somewhat resembles that of *duodecimguttata* without the protruding tip. A distinct keel is present on the ventral apical portion of the median lobe. Fields *a* and *b* are strongly microtricheate and *c* is normal. Sclerites 1, 2, 3, 4, and 6 are of the general shape and size. The sclerite between 2 and 6 is large. Sclerite 5 is barely visible and only occurs as a small roughened area.

Discussion

It is difficult to fix the genitalia of each species in the same relative position for drawing purposes. Thus sclerites that are of the same shape but drawn in different positions may appear to be different from one another. The shapes of sclerites 2, 3, 4 (excepting that of *hirticollis*), and 6 are remarkably constant throughout the North American *maritima* group. This uniformity in sclerite shape sets these species apart as a unit from other *Cicindela* groups. Some interspecific differences of the internal sac are evident, however. These are: shape and size of sclerite 1; presence and size, or absence of the sclerite between 2 and 6; presence and condition, or absence, of sclerite 5. The shape of the median lobe is diagnostic for each species, particularly the form of the apical region viewed from the dorsal or ventral sides.

Median lobes and internal sacs of specimens taken in the hybrid region of *duodecimguttata* and *oregona* were examined. It was found that the form of the apex of the median lobe changed through intermediate shapes from pure *duodecimguttata* to pure *oregona*.

TAXONOMY OF THE NORTH AMERICAN COMPONENTS OF

THE *CICINDELA MARITIMA* GROUP

Diagnosis of the Group

At the present time there is no generally accepted definition of the *maritima* group (*repanda* group, in part). Leng (1902) defined the *repanda* group on the basis of external characters in which *repanda, hirticollis, oregona,* and *duodecimguttata,* were brought together, but *limbata* and *bellissima* were excluded. Casey (1913) formed the *repanda* group on the basis of body size and shape of humeral lunule. The species *limbata* and *bellissima* were not included, and *hirticollis* was regarded as constituting a closely related but separate group. Papp (1952) used characters of the internal sac of
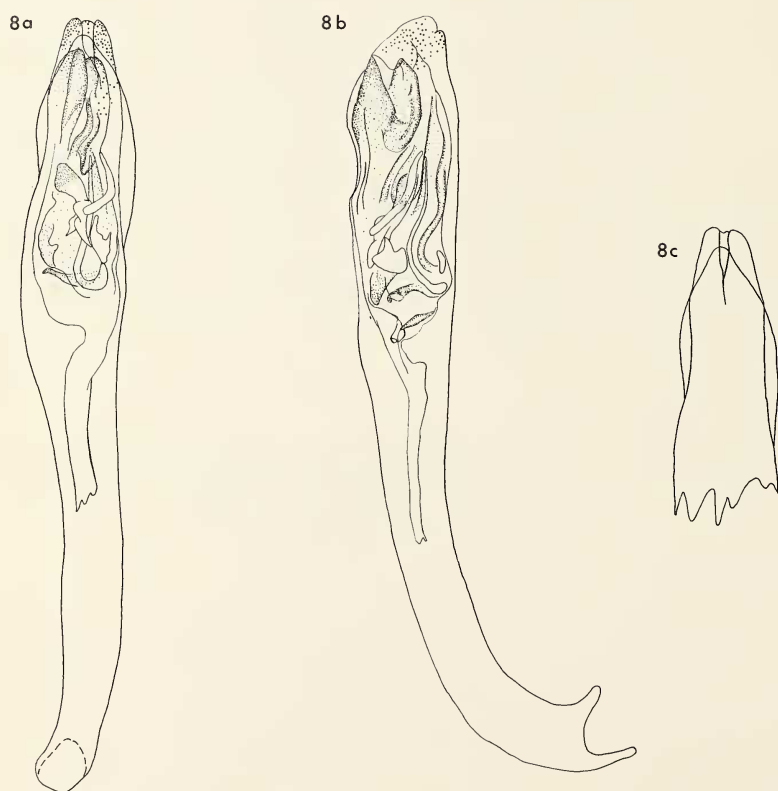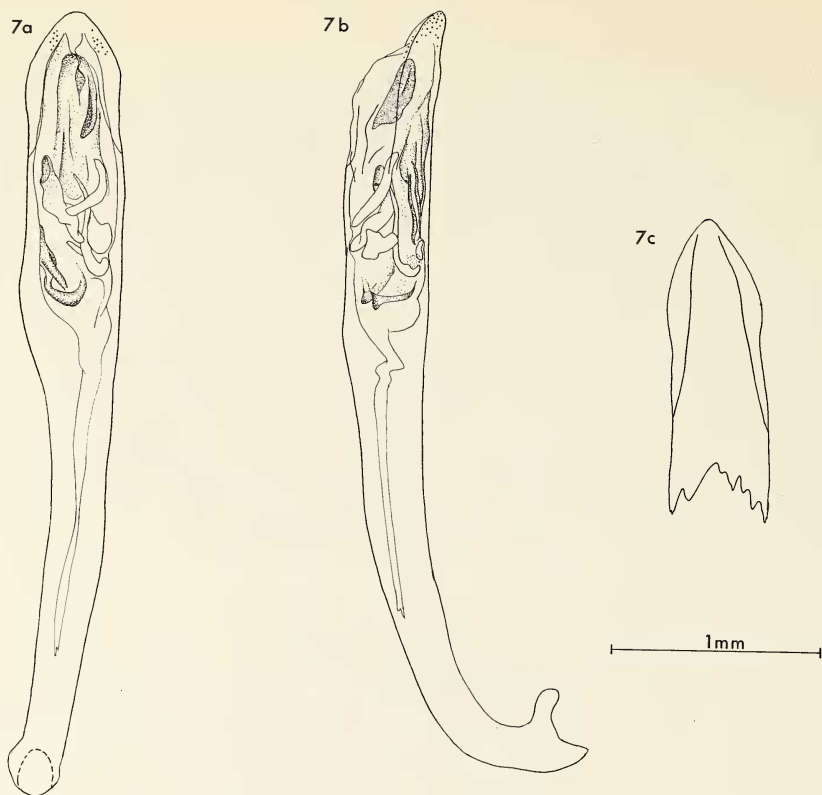
Fig. 7. Median lobe and inverted internal sac of *Cicindela columbica*. 7a, dorsal aspect; 7b, left lateral aspect; 7c, apical portion, dorsal aspect.

Fig. 8. Median lobe and inverted internal sac of *Cicindela hirticollis*. 8a, dorsal aspect; 8b, left lateral aspect; 8c, apical portion, dorsal aspect.
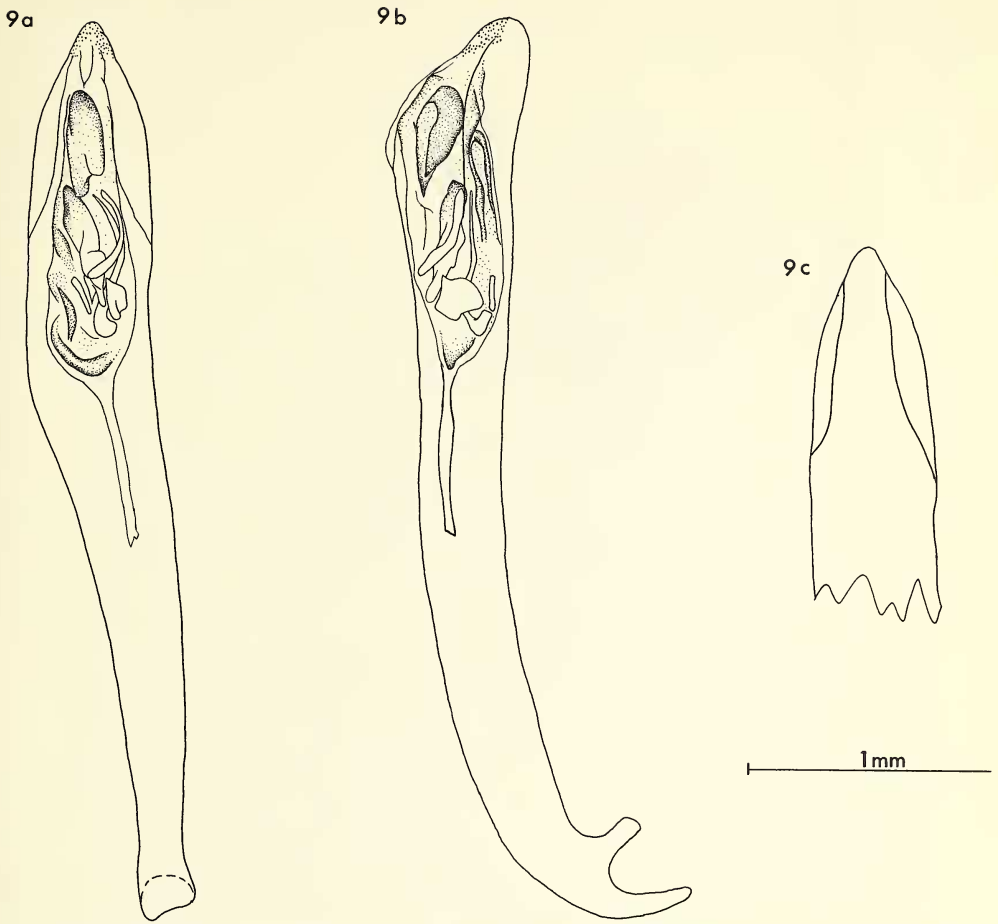
Fig. 9. Median lobe and inverted internal sac of *Cicindela theatina*. 9a, dorsal aspect; 9b, left lateral aspect; 9c, apical portion, dorsal aspect.

the male genitalia for grouping members of the *repanda* complex (*sensu* Leng) together with other species, which, I believe, should have been included in other species groups. The diagnosis of the North American species of the *maritima* group made by Rivalier (1954, Group IV) is followed here. Rivalier united members of the *repanda* group with *limbata* and *bellissima*, but *columbica* and *theatina* were not mentioned.

    The following combination of characters of the internal sac of the male genitalia is regarded as being diagnostic, and separates the North American species of the *maritima* group from other species groups of *Cicindela* (see fig. 10): sclerite 1, a quadrate plate lying over the base of sclerite 4 (flagellum); sclerite 2, a flat, elongate, curved strip; sclerite 3, short, rectangular, and lying to the left of sclerite 4; sclerite 6, large, twisted basally, and lightly sclerotized apically; field *a* apical in the inverted position, roughened or densely aculeate; field *b*, a finger-like projection, roughened or densely aculeate; field *c*, semi-circular shape, terminal in the everted position; chitinous tooth (defined by Papp, 1952) absent.

Fig. 10. Sclerites of the internal sac of the North American species of the *maritima* group, numbered as in fig. 1.
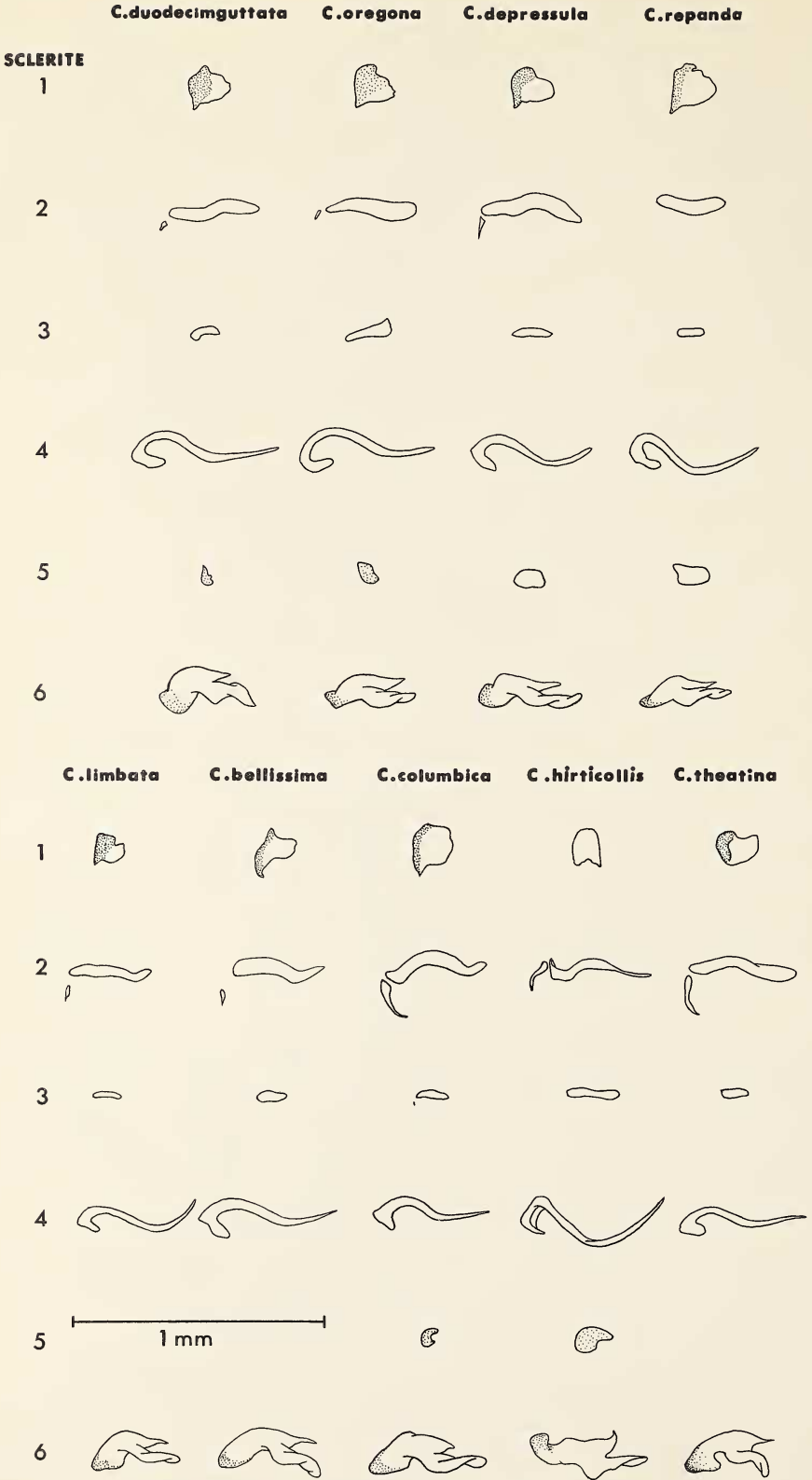
Keys to the North American Species of the *maritima* Group

Based on Non-genitalic Characters

For species marked *, reference to the median lobe of the male is advisable.

1　　　　Genae glabrous....................................... 2
　　　　Genae hairy (if hairs of the head or genae are abraded their
　　　　former positions are indicated by tiny setigerous punctures .. 6
2　(1)　Posterior tip of humeral lunule (when present) usually with
　　　　a slight anteriorly-directed hook; head with frons covered
　　　　with numerous hairs..........................*C. hirticollis* Say
　　　　(not treated in detail).
　　　　Posterior tip of humeral lunule not hooked; dorsum of head
　　　　covered sparsely with hairs;OR glabrous;OR hairs clustered
　　　　near the front inner edge of each eye...................... 3
3　(2)　Marginal band of elytron absent......................... 4
　　　　Marginal band of elytron present........................ 5
4　(3)　Cluster of one to four hairs near each eye; shoulder of
　　　　middle band (usually) smoothly rounded;vertex often with
　　　　several very small hairs........... * *C. depressula* Casey (p.　　)
　　　　Cluster of eight to 11 hairs near each eye; shoulder of
　　　　middle band (usually) raised; vertex usually glabrous..........
　　　　..............................* *C. oregona* LeConte (p.　　)
5　(3)　Frons sparsely hairy; humeral lunule elongate and markedly
　　　　oblique; posterior tip of humeral lunule nearly touching
　　　　shoulder of middle band...................... *C. bellissima* Leng
　　　　(not treated in detail).
　　　　Frons glabrous; humeral lunule short and slightly oblique;
　　　　posterior tip of humeral lunule widely separated from shoulder
　　　　of middle band.............................. *C. columbica* Hatch
　　　　(not treated in detail).
6　(1)　Humeral lunule c-shaped or in the form of two dots; elytral
　　　　markings narrowly expanded or broken..................... 7
　　　　Humeral lunule oblique; elytral markings very broad,
　　　　widely connected, or brown pigment of elytra greatly
　　　　reduced obliterating basic elytral markings................. 8
7　(6)　Form broader than *repanda*; pronotum broad; marginal
　　　　band absent or widely separated from humeral lunule..........
　　　　.......................... * *C. duodecimguttata* Dejean (p.　　)
　　　　Pronotum narrow; marginal band connected to humeral
　　　　lunule.....................................* *C. repanda* Dejean
　　　　(not treated in detail).
8　(6)　Elytra predominantly pale, elytral pattern completely
　　　　obliterated....................................... *C. limbata* Say
　　　　(not treated in detail).
　　　　Elytra predominantly dark............................... 9
9　(8)　Marginal band broad and widely connected to other elytral

markings; posterior portion of humeral lunule short............ .... *C. theatina* Rotger (not treated in detail).

Marginal band short connected only to middle band; posterior portion of humeral lunule very long............... *C. limbata* Say (not treated in detail).

Based on the Male Genitalia

1   Median lobe with apical lateral flanges narrow.............. 2
        Apical lateral flanges of median lobe broad................. 4

2 (1) Chamber of internal sac extended dorso-apically; sclerite between 2 and 6 large; sclerite 4 with a pronounced twist...... .... *C. hirticollis* Say (figs 8, 10)
        Chamber of internal sac not extended; sclerite between 2 and 6 small or absent; twist in sclerite 4 normal........... 3

3 (2) Sclerite 5 large; no sclerite between 2 and 6; part of median lobe containing internal sac short.................... .... *C. repanda* Dejean (figs 4, 10)
        Sclerite 5 normal size; sclerite between 2 and 6 small; part of median lobe containing internal sac elongate........... .... *C. oregona* LeConte (figs 2, 10)

4 (1) Apical portion of median lobe with a distinct keel along median line..................... *C. theatina* Rotger (figs 9, 10)
        Keel absent... 5

5 (4) Apex of median lobe produced into a narrow tip.............. 6
        Apex of median lobe blunt, not produced................... 7

6 (5) Sclerite 5 absent; fields *a* and *b* densely aculeate............. .... *C. bellissima* Leng (figs 6, 10)
        Sclerite 5 normal size; fields *a* and *b* lightly aculeate.......... .... *C. duodecimguttata* Dejean (figs 1, 10)

7 (5) Lateral flanges of median lobe constricted basally; sclerite between 2 and 6 large............. *C. columbica* Hatch (figs 7, 10)
        Lateral flanges of median lobe not constricted; sclerite between 2 and 6 normal size................................. 8

8 (7) Sclerite 5 absent; fields *a* and *b* densely aculeate............. .... *C. limbata* Say (figs 5, 10)
        Sclerite 5 present; fields *a* and *b* lightly aculeate............. ....*C. depressula* Casey (figs 3, 10)

The Species *Cicindela duodecimguttata* **Dejean**

Cicindela duodecimguttata Dejean 1825:73. Type locality - Amerique septentrionale. Fall 1901:308. Leng 1902:148. Blatchley 1910:34. Casey 1913:28. Horn 1915:374, and 1930:80. Stainer 1934:247. Papp 1952:515. Rivalier 1954:252. Lindroth 1955:16. Wallis 1961:20. Graves 1963:498.
Cicindela bucolica Casey 1913:28. Type locality - Aweme, Manitoba. Wallis 1961:21.
Cicindela hudsonica Casey 1916:29. Type locality - Hudson

Bay Territory. Wallis 1961:21.
Cicindela repanda edmontonensis Carr 1920:218. Type locality -
Edmonton, Alberta. NEW SYNONYMY
Cicindela repanda duodecimguttata, Horn 1930:81 (not Dejean);
Papp 1952:515.

This species is characterized by its dull brown dorsal surface, and elytral maculations (see figs 11, 13, 15). Specimens of *duodecimguttata* are usually distinguishable from specimens of the markedly similar species *repanda*. In western areas, where these species are sympatric, individuals of *duodecimguttata* have a broad prothorax, dark brown elytra, and widely interrupted marginal bands, while specimens of *repanda* have a narrower prothorax, lighter brown elytra, and the marginal bands are narrowly, or not interrupted. In eastern Canada the elytral pattern of *duodecimguttata* generally is broken but *repanda* retains full elytral maculations excepting the subspecies *novascotiae* Vaurie that occurs on the Canadian Atlantic coast (see Vaurie 1951). Differences in male genitalia however, are clear and should be used for definitive identification (see p. 91 & Lindroth 1955: 16-17).

In western Canada, populations of *duodecimguttata* occur on the edges of lakes, ponds, rivers, streams, and sloughs wherever the soil is dark and wet and consists of mixtures of sand and clay, and clay or mud. This type of habitat is preferred by *duodecimguttata* on the mainland in eastern Canada (see Leng 1902, Blatchley 1910, and Graves 1963). Lindroth (1955) in Newfoundland found *duodecimguttata* on sand and gravel, as well as on clay or humus.


Notes on Synonymy

The name *bucolica* Casey has been given to specimens of *duodecimguttata* with full elytral markings. Such specimens are common in the western prairies. Casey's *hudsonica*, the elytral pattern of which is very reduced, is a variant of *duodecimguttata*. The name *edmontonensis* Carr was proposed for a variant of *duodecimguttata* that has a narrow elytral pattern. Horn (1930) treats *repanda* as a larger race of *duodecimguttata* and *bucolica* as a lesser form of *repanda*. Evidence for this synonymy is presented in the following section on geographic variation.

Geographic Variation

This species inhabits a territory that extends from the eastern front of the Rocky Mountains to the Atlantic seaboard, and from the Northwest Territories to Alabama (fig. 17). Throughout the range of *duodecimguttata*, except for the zone of intergradation with *oregona*, two easily observed characters vary geographically: color of the dorsal surface of the body and elytral pattern. Variation in both features has been examined quantitatively. Variation in length of elytra has also been studied.

Average lengths of elytra, from the tip of the scutellum to the end of the elytral spine, were calculated for males and females from the 20
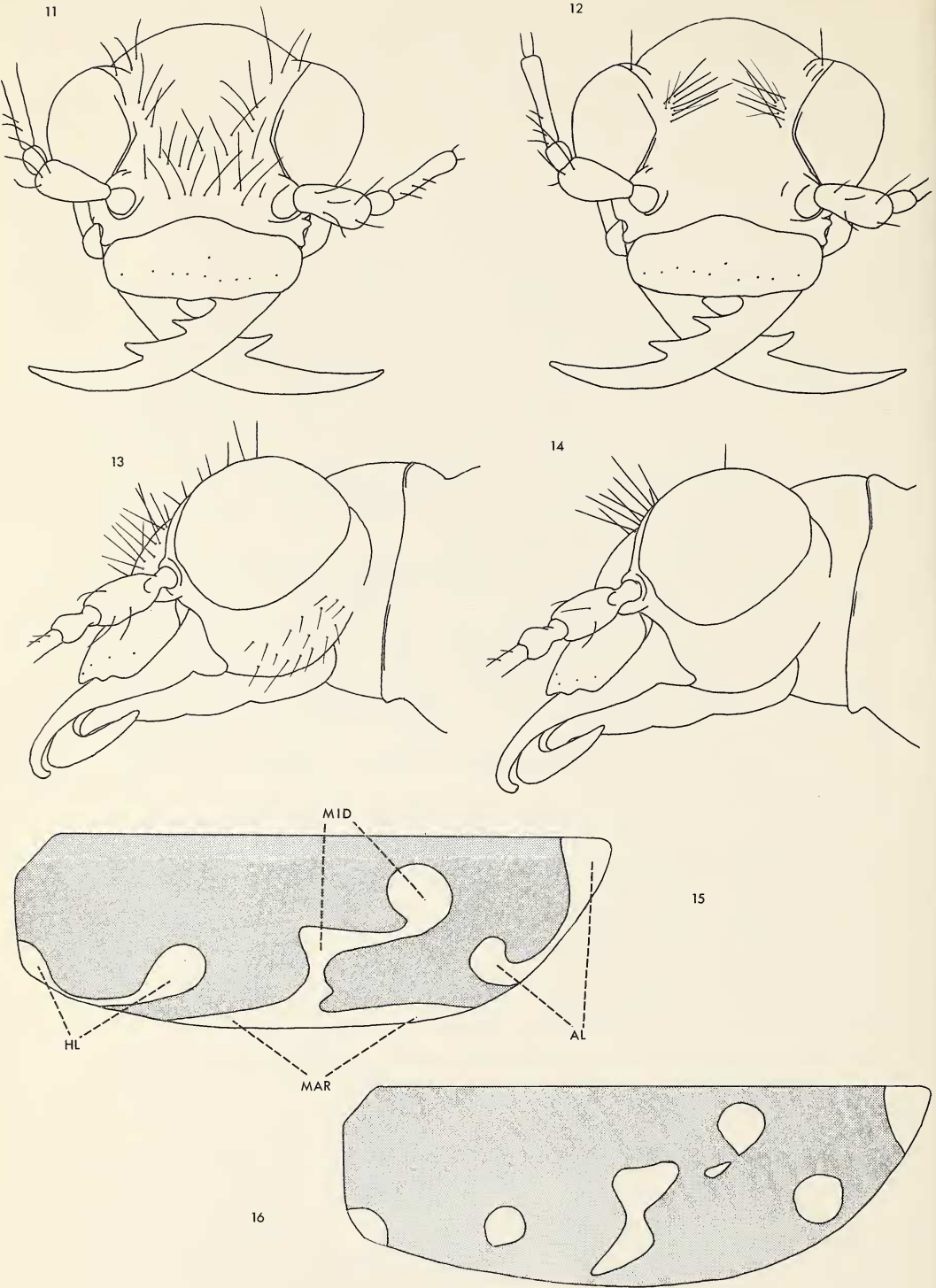
Figs 11 and 12. Anterior views of the heads of *C. duodecimguttata* and *C. oregona*. Figs 13 and 14. Lateral views of the heads of *C. duodecimguttata* and *C. oregona*. Figs 15 and 16. Left elytra of *C. duodecimguttata* and *C. oregona*: HL, humeral lunule; MAR, marginal band; MID, middle band; AL, apical lunule.

localities listed in table 3. Character gradients are irregular and do not conform with latitudinal, longitudinal, or altitudinal changes. The mean lengths of elytra range from 6.57 mm to 7.60 mm for males, and 7.11 mm to 8.22 mm for females. Average elytral lengths of males and females from the island of Newfoundland (Harmon Field) are not larger than those of corresponding sexes from coastal localities of the adjacent mainland such as Bathurst, New Brunswick.

There are no color differences between sexes of *duodecimguttata*. Males and females are usually dull brown dorsally, metallic blue-green ventrally, and the thoracic pleura are coppery. The dorsal surface is the only area that is subject to color variation. In most regions the dorsum is dull brown, but in eastern Canada and United States, color varies.

Specimens from seven localities on or near the Atlantic seaboard were examined for color of the dorsal surface; the results are listed in table 1. Brown specimens are most abundant in all of the population samples, followed in number by brown-green or green and finally blue individuals.

The most variable maritime population sample is one collected at Yarmouth, Nova Scotia. The entire color range is represented. Brown specimens account for 56 per cent of the sample. Green, brown-green, and blue individuals follow in number in that order. Blue specimens are absent from the Goose Bay, Labrador, and Harmon Field, Newfoundland samples both of which are composed mainly of brown members, followed by brown-green and green. Only brown individuals occur in the Bathurst, New Brunswick population sample. Except for one green specimen from Keene Valley, New York, the inland samples are made up entirely of brown specimens. Green specimens are not uncommon in coastal populations of species of the *maritima* group (see *o. oregona* and *o. novascotiae* Vaurie 1951).

The elytral pattern is fully developed in some *duodecimguttata* individuals and almost absent in others. The four main components of the elytral pattern vary independently. There were assigned numerical values to form a compound character index for analysing variation in elytral pattern. If all markings are complete a high score is assigned (maximum value 11), and if the markings are greatly reduced a low value is assigned (minimum value 0). Markings that range between complete and reduced are given intermediate values. The components of the elytral pattern are illustrated in fig. 15 and their assigned values are given in table 2. As many eastern *duodecimguttata* specimens have maculations typical of *oregona*, the compound character index used in this section was not employed in the hybridization section. A compound character index (hybrid index), based on the elytral pattern, was determined for each specimen of 20 population samples from different localities. Results are presented in table 3. The average index value for each sample is indicated in fig. 17. The samples are arrayed in five transects so that geographical variation in elytral maculations may be more clearly appreciated. Three transects - A-A', B-B', and C-C' - are run from west to east, while two - D-D', and E-E' - are oriented north to south.

Fig.17-Distribution of *C. duodecimguttata* and average compound character index values for 18 population samples.

TABLE 1 - Variation in color of dorsal surface of *C. duodecimguttata* from seven eastern N. American localities.

Locality	No. Brown	No. Brown-green	No. Green	No. Blue	Total No.
Goose Bay, Labr.	16	12	1	0	29
Harmon Field, Nfld.	41	14	4	0	59
Bathurst, N. B.	19	0	0	0	19
Yarmouth, N. S.	29	8	11	4	52
Duparquet, Que.	17	0	0	0	17
Keene Valley, N. Y.	45	0	1	0	46
Jeannette, Pa.	31	0	0	0	31

TABLE 2 - Values assigned to elytral markings of *C. duodecimguttata* specimens for determination of compound character indices.

Elytral Markings	Values			
	0	1	2	3
Humeral lunule	1 dot	2 dots	broken	full
Middle band	1 dot	2 dots	broken	full
Apical lunule	1 dot	2 dots	broken	full
Marginal band	absent	trace	full	-

An average index reduction from west to east is seen in the A-A' transect. The mean values 9.73 and 9.39 of the samples that represent Christopher Lake, Saskatchewan and The Pas, Manitoba, respectively, indicate full elytral markings. The mean index change per mile between these localities is about 0.00160. The mean index for the population sample from Ogoki, Ontario is 6.22 which is a change of 0.00488 index units per mile from that of The Pas, Manitoba. The trend is less marked between Ogoki, Ontario and Duparquet, Quebec the rate of change being 0.00320 index units per mile. A change in average index value of 0.00133 occurs between Duparquet, Quebec (4.94) and Bathurst, New Brunswick (4.11), and a change of 0.00127 occurs between Bathurst, New Brunswick and Harmon Field, Newfoundland (4.54).

Average index values of the six population samples in transect B-B' complement the trend shown in A-A'. Elytral maculations are quite full in western localities as shown by average index values: Lethbridge, Alberta, 10.12; Bottineau County, North Dakota, 9.88; and Minnesota, 9.44. The rate of mean index change per mile between Lethbridge, Alberta and Bottineau County, North Dakota is only 0.00041 and increases slightly to 0.00130 between Bottineau County, North Dakota and Minnesota. However, the average index value for the Cheboygan, Michigan specimens is markedly less than that of the Minnesota sample, the rate of change being 0.00776 index units per mile. This is approximately six times the rate of change between Bottineau County, North Dakota and Minnesota. Mean index differences between eastern population samples are slight. Average values for areas follow: Cheboygan, 5.79; Keene Valley, New York, 5.21; and Yarmouth, Nova Scotia, 5.10, showing a reduction in the elytral pattern.

The southernmost west-east transect, C-C', comprises the following population samples and average index values: Bennett, Nebraska, 6.03; St. Louis, Missouri, 4.79; and Jeannette, Pennsylvania, 5.77. The mean index decreases 0.00355 units per mile between Bennett and St. Louis while between St. Louis and Jeannette there is a mean increase of 0.00158 units per mile.

Transect D-D' is oriented north to south near the western limits of the range of this species. The pattern of the elytra tends to increase

TABLE 3 - Frequency distribution of compound character index values of specimens of *C. duodecimguttata* from 20 localities.

Localities	1	2	3	4	5	6	7	8	9	10	11	N
Fort Smith, N. W. T.			4	2	8	7	10	12	32	70	17	162
Lethbridge, Alta.					2	3	3	6	27	162	107	310
Christopher L., Sask.			1			1	2	2	6	33	12	57
The Pas, Manitoba					1	2	1		3	11	5	23
Bottineau County, N. D.					2		1	5	6	40	20	74
Minnesota					1	4	6	4	12	28	18	73
Wolsey, S. D.							1		1	11	4	17
Bennett, Nebraska			9	9	13	8	18	12	2	3		74
St. Louis, Mo.			3	8	4	1	2			1		19
Texas			3	6	5	2	1	2	1			20
Ogoki, Ontario		1	4	7	7	9	5	4	2	7		46
Cheboygan Co., Mich.			10	15	25	21	9	10	5		5	100
Oktibbeha Co., Miss.		1	61	12	2	4		1				81
Duparquet, Quebec	1		4	3		8		2				18
Keene Valley, N. Y.			8	12	9	5	3	1	3	1	1	43
Jeannette, Pa.			4	7	6	4	4	1	2	2	1	31
Goose Bay, Labr.		1		6	11	2	3	2	1	3		29
Bathurst, N. B.			8	6	3		1	1				19
Yarmouth, N. S.		1	4	15	15	10	3	2	1	1		52
Harmon Field, Nfld.		2	15	20	9	6	2	3	1		1	59

north to south in the first part of the transect as follows: Christopher Lake 9.71, Bottineau County 9.88, and Wolsey, South Dakota 10.00. The spatial mean change in index units between these population samples is negligible in contrast to that which occurs between Wolsey and Bennett (0.01498). The mean index value at Bennett is 6.03, and it is 5.10 for Texas. The three northern localities therefore have samples with full elytral markings, while specimens of the two more southerly localities have reduced maculations, a sharp change occurring between Wolsey and Bennett.

    A clinal north to south fragmentation in maculation of the elytra is evident in transect E-E'. Ogoki, Cheboygan, St. Louis, and Oktibbeha County, Mississippi have population samples with mean index values of 6.22, 5.79, 4.79, and 3.40 respectively. The rate of increase in mean index units per mile is 0.00101 between Ogoki and Cheboygan, 0.00170 between Cheboygan and St. Louis, and 0.00376 between St. Louis and Oktibbeha County, Mississippi.

    The population samples can be separated into two geographic groups by areas of marked rates of change in mean index values. The

greatest differences in average index values are between The Pas, Manitoba and Ogoki, Ontario; between Minnesota and Cheboygan County, Michigan;and between Wolsey, South Dakota and Bennett, Nebraska. The species therefore may be divided into northwestern populations that have complete elytral markings, and southern and eastern groups that exhibit a more or less interrupted elytral pattern. However, the two aggregates of populations are not subspecifically distinct. A separation on the basis of the 75 per cent rule cannot be made becaues of extensive overlap in range of variation between the two groups of populations.

Breakdown of the elytral pattern has probably occurred independently in *duodecimguttata*, *repanda, depressula*, and *oregona* and if so this is a good example of parallel evolution. Perhaps the breakdown of elytral pattern in *duodecimguttata* is the result of a mutation that has spread throughout most populations except for those in the west.

Canada. ALBERTA: Andrew, 3; Beaver Hill Lake, 1; Bilby, 14; Chin, 8; Cooking Lake, 7; Cypress Hills, 2; Doussal, 1; Drayton Valley, 4; Edmonton, 95; Falles, 1; Flatbush, 1; Fort Chipewyan, 1; Halfway House, 3; Jct. Rte. 39 and North Saskatchewan River, 11; Lake Cardinal, 2; Lesser Slave Lake (east end), 1; Lethbridge (St. Mary's River), 5; Lethbridge (Six-mile Coulee), 310; Louis Bull Reservation, 3; McMurray, 18; Medicine Hat, 5; mile 7 on Smith-Fitzgerald Road, 1; Redwater, 2; Stirling Lake, 1; Tilley, 1; Tofield, 19; Vilna, 1; Wabamun, 3. LABRADOR: Goose Bay, 29. MANITOBA: Aweme, 12; Baldur, 1; Beaver Lake, Riding Mountain, 2; Berens River, 9; Birtle, 1; Brandon (15 miles south), 2; Carberry (5 miles west), 1; Clear Lake, Riding Mountain, 2; Dauphin, 5; Delta, 3; Douglas, 2; Gladstone, 2; Glenboro, 1; Grunthal, 1; Hilton (6 miles south), 21; Holland, 2; Husavick, 3; Kelwood, 1; The Pas, 23; Magnuls, 1; Makinock, 5; Marchand, 1; Max Lake, Turtle Mountain, 10; Melita, 1; mile 360, Rte. 10, 1; Morris, 1; Ninette, 25; Norgate (5 miles west), 5; Oak Lake (4 miles west), 1; Red River, 1; Red Rock Lake, 1; Rennie (15 miles east), 1; Riding Mountain, 7; Rounthwaite, 1; Sandilands, 3; Shilo (5 miles south west), 4; Shoal Lake, 1; Silver Falls, 2; South Junction, 3; Stonewall, 1; Treesbank, Assiniboine River, 35; Vassar, 1; Victoria Beach, Lake Winnipeg, 8; Wanless, 1; Wasagaming, 1; Watson's Lake, 1; Waugh, 1; Westbourne, 1; Whitemouth, 1. NEW BRUNSWICK: Apohaqui, 1; Bathurst, 19; Chipman, 6; Penobsquis, 3; St. John, 1; Sackville,3; Shediac, 10. NEWFOUNDLAND: Bay of Islands, 4; Bay St. George, 13; Codnoy, 11; Deer Lake, Humber River, 2; Gander, 14; Harmon Field, 59. NORTHWEST TERRITORIES: Fort Smith, 163; Hay River (Great Slave Lake Shore), 1; Seven Mile Lake (26 miles west Fort Smith), 6; Resolution, 5. NOVA SCOTIA: Armdale, 3; Baddeck, 2; Barrington Passage, 1; Boisdale, 16; Cape Breton, 35; Cow Bay, 29; Bigby, 1; Great Village, 8; Halifax, 1; Ingramport, 5; Kedgemakooge Lake, 2; Kentville, 11; Lockeport, 2; North Sidney, 9; Port Maitland, 36; Queens, 2; Truro, 10; Weymouth, 1; Wilmot, 1; Yarmouth, 52. ONTARIO: Agawa Bay, Lake Superior, 1; Coniston, 3; DeCew Falls, 1; Goderich, 1; Gravenhurst, 1; Hamilton, 2; Hearst (65 miles west), 23; Hudson Bay, 1; Ingolf, 9; James Bay, 1; Kearney, 6; Kenora (14 miles east), 1; Lake of the Woods, Harris Hill, 2; Loleo, 1; Minnitaki, 1; Moose Factory, 6; Ogoki, 46; Ojibway, 1; One Sided Lake, 2; Ottawa, 2; Port Arthur, 3; Powasson, 2; Sibley Provincial Park, Middlebrun Bay, Lake Superior, 7; Sudbury, 1; Toronto, 5; Ventnor, 2; Woodtick Island, 1. QUEBEC: Baie Comeau, 1; Cap Rouge, 1; Cascapedia, 2; Charlevoix County, 4; Duchesnay, 6; Duparquet, 17; Gaspe, 5; Joliette, 2; Knowlton, 2; Lachute, 2; Ladysmith, 1; Lake Blanch, 12; Lac Opasatika, 1; Mont Joli, 2; Mont Lyall, 2; Montreal, 2; Natashquan, 1; Otter Lake, 12; St. Alexandre, 1; Ste. Anne de Monts, 1; Val Morin, 1. SASKATCHEWAN: Big River, 16; Broadview, 4; Candle Lake, 3; Ceylon, 1; Christopher Lake, 24; Cut Knife, 4; Estevan, 2; Fish Lake, 1; Glaslyn, 3; Good Spirit, 10; Holbein, 1; Kenosee, 11; Lake Manitou, 1; Neat Frys, 9; Pike Lake, 1; Pike Lake Park, 41; Regina, 1; Saskatoon, 22; Val Marie, 2; Waskisiu Lake, 10; White Fox, 12; Yorkton, 2.

United States. ALABAMA: Chilton County: Coosa River, 1. Tuscaloosa County, 1. ARKANSAS: Boone County: Harrison, 2. Lawrence County, 1. Washington County: Fagett, 1. Localities of unknown counties: Ozark Mountains, 11. COLORADO: Fremont County: Coal Creek, 1. CONNECTICUT: Litchfield County: Cornwall, 3; Litchfield, 2; Torrington, 3; Twin Lakes, 4; Washington, 2. New Haven County: Meriden, 7. DELAWARE: New Castle County: Newark, 6. GEORGIA: Fulton County: Atlanta, 8; East Point, 1. Habersham County: Cornelia, 1. Localities of unknown counties: Georgia, 1. ILLINOIS: Champaign County: Champaign, 1; Urbana, 4. Cook County: Chicago, 17; Cook County, 2; Flossmoor, 3; Palos Park, 2; Summit, 10. Fayette County: Ramsey, 2. Lake County: Antioch, 1; Cedar Lake, 3; Lake County, 1; Waukegan, 3. McHenry County: Algonquin, 3; McHenry, 1; Richmond, 3. McLean County: Bloomington, 1; Normal, 2. Macon County: 1. Marshall County: Taluca, 1. Ogle County: White Pines Forest, 6. Peoria County: Peoria, 4. Perry County: Pyem, 1. Piatt County, Atwood, 1. Putnam County: 2. Randolph County: Chester, 3. Rock Island County: Moline, 1. Union County: Ware, 3. Will County: New Lenox, 1. Williamson County: Crab Orchard Lake, 1. Localities of unknown counties: Dune Park, 1. Edgebrook, 16. Funks Grove, 4. Illinois, 1. Rock, 1. INDIANA: Cass County: 1. Gibson County: 2. Jefferson County: Hanover, 1. Knox County: Vincennes, 1. Porter County: Beverley Shores, 1. Posey County: 3. Starke County: North Judson, 12. Tippecanoe County: Lafayette, 3. Localities of unknown counties: Lake Station, 1. Mineral Springs, 3. Pine, 1. T.R.P. Indiana, 1. IOWA: Boone County: Boone, 27. Cerro Gordo County: Clear Lake, 1. Clayton County: Guttenberg, 1. Dickinson County: Lake Okoboji, 3. Henry County: Mount Pleasant, 1. Howard County: Elma, 1. Johnson County: Iowa City, 4. Lee County: Fort Madison,1. Story County: Ames, 2. Woodbury County: Sioux City, 1. Localities of unknown counties: Iowa, 1. Silver Lake, 1. KANSAS: Atchison County: Atchison, 3. Bourbon County: Fort Scott, 5. Coffey County: Burlington, 1. Douglas County: 3. Ellis County: 1; Hays, 1. Johnson County: Argentine, 14. Leavenworth County: Leavenworth, 7. Pottawatomie County: Onaga, 8. Riley County: 1. Saline County: Salina, 1. Shawnee County: Topeka, 11. Trego County: Wakeenay, 1. Localities of unknown counties: Central Kansas, 1. KENTUCKY: Localities of unknown counties: Kentucky, 3; Kentucky near Cincinnati, Ohio, 1. Maine: Hancock County: Bar Harbor, 1; Mount Desert, 6; Seal Harbor, 7. Kennebec County: Monmouth, 12. Piscataguis County: Greenville, 1; Mount Katahdin, 1. York County: Agamenticus, 2. Localities of unknown

counties: Bass Harbor, 2; Maine, 1; Pleasant Ridge, 5; Wales, 2. MARYLAND: Allegheny County: Mount Savage, 4. MASSACHUSETTS: Berkshire County: Benedict Pond, 2; Lenox, 4. Bristol County: Rehoboth, 2. Middlesex County: Framingham, 19; Sherborn, 9. Norfolk County: Sharon, 1. Plymouth County: 3. Suffolk County: Cambridge, 1; Medford, 1; Stoneham, 1. Worcester County: Southboro, 2. MICHIGAN: Alger County: 2; Onota Twp., 10. Allegan County: Allegan State Forest, 1; Rabbit River, 1. Alpena County: Alpena, 1; Squaw Bay, 2. Arenac County: White Stone Point, 1. Berrien County: Sawyer Dunes, 1. Cass County: 1. Charlevoix County: Beaver Island, 1; Thumb Lake, 1. Cheboygan County: 16; Douglas Lake, 84. Chippewa County: Marquette N.F., 1; Neebish Island, 4. Clare County: 8-Point Lake, 1. Delta County: Garden, 1. Genesee County: Davison T.W.P., 1; Flint, 1. Gogebic County: 12; Black River Park, 4. Huron County: Pte. Aux Barques, 2; Port Austin, 1; Sand Point, 1. Ingham County: 1. Ionia County, 1. Iosco County: 2; State Game Refuge, 1. Keweenaw County: Copper Harbor, 1; Eagle Harbor, Lake Superior, 10; Manganese Lake, 11. Lapeer County: Hadley T.W.P., 1. Mackinac County: 1; St. Ignace, 3. Marquette County: Huron Mountains, 12; Marquette, 1. Menominee County: Daggett, 1. Monroe County: Erie, 1. Montmorency County: 1. Ontonagan County: Gogebic Lake, 15. Otsego County: 2; Vanderbilt, 1. Schoolcraft County: Germfask, 1. Tuscola County: Bay Park, 2. Wayne County: Detroit, 6. Washtenaw County: Ann Arbor, 12. Localities of unknown counties: Pcn. Ind., 1; Michigan, 2. MINNESOTA: Aitkin County: Aitkin, 1. Anoka County: 2. Becker County: 5. Beltrami County: Waskish, 3. Carlton County: Moose Lake, 3. Carver County: Lake Waconia, 2. Clearwater County: 14; Gonvick, 1. Hennepin County: 1; Minneapolis, 2. Koochiching County: Rainy Lake, 3. Lac Qui Parle County: 3. Lake County: South Kawishiwi, 1. Lake of the Woods County: Williams, 1. Le Sueur County: 1. Nicollet County: St. Peter, 5. Renville County: Bird Island, 1. Roseau County: Roseau, 2. St. Louis County: Duluth, 2. Scott County: Jordan, 1. Stearns County: Koronis Lake, 6; Rice Lake, 10. Traverse County: 3. Wilkin County: Rothsay, 1. MISSISSIPPI: Oktibbeha County: 12; A & M College, 72. Tippah County: Tiplersville, 2. MISSOURI: Caldwell County: Hamilton, 13. Carter County: Van Buren, Ozarks Mountains, 2. Greene County: Springfield, 2; Willard, 8. Linn County: 1. Pike County: Louisiana, 7. St. Louis County: St. Louis, 19; Valley Park, 2. MONTANA: Cascade County: Ulm, 1. Chouteau County: Fort Benton, 1. Hill County: Fresno, 2. Roosevelt County: Brocton, 1. Teton County: Chouteau, 3. Toole County: Dunkirk (8 miles south), 5. NEBRASKA: Dawes County: Wayside, 5. Lancaster County: Bennet, 73; Lincoln, 25; Malcolm, 31. Sarpy County: Bellevue, 1. NEW HAMPSHIRE: Caroll County: Ellis River Road, Jackson, 1; Wildcat Bank, Jackson, 1. Cheshire County: Jaffrey, 2. Coos County: Gorham, Peabody River, 4; Jefferson, 25; Israel River, Jefferson, 10. Grafton County: Twin Mountain, 21. Hillsboro County: Antrim, 1. Sullivan County: Meriden, 12. Localities of unknown counties: Glen House, White Mountains, 2; Martin Loe'n, White Mountains, 3; New Hampshire, 4; White Mountains, 1. NEW JERSEY: Bergen County: Ramsey, 1. Cape May County: Ocean City, 3. Essex County: South Orange, 1. Hudson County: Arlington, 6; Snake Hill, 5. Middlesex County: Jamesburg, 10; Milltown, 2. Passaic County: Paterson, 1. Salem County: Canton, 1. Sussex County: Lake Hopatcong, 1. Localities of unknown counties: Frieses Mill, 1; Manchester, 1; New Jersey, 2. NEW YORK: Cortland County: McLean Bogs, 1. Delaware County: Stamford, 3. Erie County: Buffalo, 1. Ebenezer, 1. Essex County: Ausable Lakes, 1; Elizabeth Town, 1; Heart Lake, 5; Jay Mountains, 1; Keene Valley, 46; Lake Golden, 1; Mount Whiteface, 3; Wilmington, 4. Franklyn County: Duane, 1. Fulton County: 1. Genesee County: Bergen, 6. Hamilton County: Lake Pleasant, 4; Racquet Lake, 3. Nassau County: Freeport, 1. New York County: New York City, 5. Niagra County: Lockport, 3. Onondaga County: White Lake, 5. Orangelo County: Pine Island, 3. Oswego County: Minetto, 2. Queen's County: Far Rockaway, 1. Richmond County: Clover Valley, Staten Island, 1; Hugenot, Staten Island, 1. St. Lawrence County: Cranberry Lake, 2. Tompkins County: Ithaca, 16. Warren County: Lake George, 1; Stamford, 3. Localities of unknown counties: Big Island, 3; Clearwater, 1; Luzerne, 1; Quaker Hill, 2. NORTH CAROLINA: Buncombe County: Black Mountains, 1. Guilford County: Jamestown, 1. Mecklenburg County: Charlotte, 2. Moore County: Manly, 2; Southern Pines, 2. Orange County: Chapel Hill, 2. Localities of unknown counties: Morrison, 6. NORTH DAKOTA: Benson County: 2. Bottineau County: 73; Lake Metigoshe, Turtle Mountain, 8; Omemee, 3. Burleigh County: 3; Bismark, 1. Burke County: 4. Cass County: Fargo, 1. Cavalier County: 4. Divide County: 4. Eddy County: New Rockford, 14; Sheyenne River, 3. Kidder County: Tappen, 1. Logan County: 4. McHenry County: 14. McLean County: 1. Morton County: 3. Nelson County: 4; Stump Lake, 3. Pembina County: 1. Ransom County: 3. Rawsey County: 1. Renville County: 8. Richland County: 2. Rolette County: 10; Golden Lake, Turtle Mountain, 2. Sheridan County: 2. Ward County: 4. Wells County: 1. Williams County: 3. Localities of unknown counties: Jarves Lake, 1; Mooreton, 3. OHIO: Ashtabula County: Ashtabula, 2; Jefferson, 17. Delaware County: 1. Franklin County: Columbus, 10. Gallia County: Vinton, 3. Hamilton County: Cincinnati, 4. Hocking County: 1. Licking County: Bowling Green Trail, 4; Newark, 1. Localities of unknown counties: Crane Hollow, 1. OKLAHOMA: Blaine County: Roman Nose State Park, 3. Cleveland County: Norman, 4. Garfield County: Enid, 1. Johnston County: 1. Kay County: Newkirk, 2. Kingfisher County: Kingfisher, 1. Murray County: Sulphur, 5. Noble County: Perry, 7. Payne County: Lake Carl Blackwell, 1; Stillwater, 1. Localities of unknown counties: Blue Jacket, 3; Centralia, 1; Wyandotte, 1. PENNSYLVANIA: Allegheny County: 5; Fair Oaks, 2; Westview, 1. Crawford County: Meadville, 1. Cumberland County: Mount Holly, 1. Delaware County: 4; Lansdowne, 4. Forest County: Endeavor, 1. Mercer County: Sharpsville, 1. Montgomery County: 1. Philadelphia County: Lawndale, 1; Philadelphia, 3. Warren County: Bear Lake, 1. Westmoreland County: Jeannette, 31. Localities of unknown counties: Castle Rock, 7; Pennsylvania, 1; Springfield, 2; Wali, 1. RHODE ISLAND: Providence County: Elmwood, 5. Washington County: Misquamicut, 2. SOUTH CAROLINA: Greenville County: Greenville, 1. Pickens County: Clemson College, 5. Richland County: Columbia, 11. SOUTH DAKOTA: Beadle County: Wolsey, 17. Fall River County: Hot Springs (5 miles south), 1. Lawrence County: Deadwood, 1; Savoy, 2. Meade County: Sturgis, 3. Moody County: Colman, 2. Pennington County: Rapid City, 1. Localities of unknown counties: South Dakota, 1. TENNESSEE: Knox County: Knoxville, 2. Pickett County: 1. TEXAS: Blanco County: 1. Dallas County: 1; Dallas, 10. Randall County: Canyon, 1. Washington County: Burton, 2. Localities of unknown counties: Cyp. Mills, 1; Texas, 4. VERMONT: Bennington County: Mount Equinox, 2. Localities of unknown counties: Vermont, 1. VIRGINIA: Bath County: Warm Springs, 4. Lee County: Pennington Gap, 1. Nansemond County: Suffolk, 2. Localities of unknown counties: Black Pond, 1; Virginia, 1. WEST VIRGINIA: Wyoming County: Pineville, 3. WISCONSIN: Bayfield County: Lake Namekagon, 1. Clark County: Wordon Township, 1. Dane County: 2. Dodge County: Beaver Dam, 10. Douglas County: Superior, 1. Kewaunee County: Kewaunee, 1. Milwaukee County: Milwaukee, 1. Vilas County: Tenderfoot Lake, 1. Walworth County: Allens Grove, 2. Waukesha County: Oconomowoc, 1. Waupaca County: Waupaca, 1. Wood County: Cranmoor, 4. Localities of unknown counties: Walker, 1; Wisconsin, 1. WYOMING: Crook County: Alva (6 miles east), 3; Devil's Tower, 6. Sheridan County: Sheridan (8 miles north west), 4.

The Species *Cicindela oregona* **LeConte**

Cicindela oregona oregona LeConte 1857:41. Type locality - Oregon Territory
  and northern California as far as San Francisco. Fall 1901:308.
  Leng 1902:149. Casey 1913:29. Horn 1915:377, and 1930:82.
  Varas Arangua 1928:247. Tanner 1929:83. Papp 1952:514. Hatch
  1953:41 (see Hatch 1953 for more references to *o. oregona*).
  Cazier 1954:242. Rivalier 1954:252. Wallis 1961:22.
  Cicindela guttifera , Fall 1901:308.
  Cicindela guttifera , Leng 1902:150.
  Cicindela depressula scapularis Casey 1909:272. Type locality - California.
  Cicindela guttifera sonoma Casey 1913:29. Type locality - California
  (maritime regions north of San Francisco). Horn 1915:378.
  Cicindela quadripennis Casey 1913:30. Type locality - Hawthorne,
  Nevada. Horn 1915:378.
  Cicindela ovalipennis Casey 1913:30. Type locality - Hawthorne,
  Nevada. Horn 1915:378.
  Cicindela oregona scapularis, Horn 1915:378.
Cicindela oregona guttifera LeConte 1857:42. Type locality - New Mexico.
  Leng 1902:41. Horn 1915:378, and 1930:82. Varas Arangua 1928:
  250. Tanner 1929:83. Cazier 1954:242. Wallis 1961:22.
  Cicindela sterope Casey 1913:28. Type locality - Kansas. Horn 1915:
  378.
  Cicindela audax Casey 1913:29. Type locality - Colorado. Horn 1915:
  378.
  Cicindela guttifera , Casey 1913:29.
  Cicindela oregona oregonella Casey 1924:16. Type locality - Parowan,
  Utah.
  Cicindela duodecimguttata, Hatch 1953:38 (not Dejean).
Cicindela oregona guttifera x *Cicindela oregona maricopa*
  Cicindela provensis Casey 1924:15. Type locality - Parowan and Provo
  Canyon, Utah.
  Cicindela provensis mormonella Casey 1924:15. Type locality - Eureka,
  Provo Canyon, Parowan and Vineyard, Utah.
  Cicindela provensis nephiana Casey 1924:16. Type locality - Parowan,
  Utah.
  Cicindela oregona maricopa, Tanner 1929:83 (not Leng).
Cicindela oregona maricopa Leng 1902:150. Type locality - Phoenix, Arizona.
  Horn 1915:378. Horn 1930:82.
  Cicindela guttifera maricopa , Casey 1913:27. Varas Arangua 1928:250.
Cicindela oregona navajoensis Van Dyke 1947:155. Type locality - Kayenta,
  Arizona.

On the basis of a patch of hairs confined to the front inner edge of
each eye this species may be distinguished from all other tiger beetles of
the *maritima* group, except *depressula* and female *scutellaris* Say (see figs 12,
14, 16). Female *scutellaris* and *oregona* specimens usually can be distinguish-

ed from each other simply by noting the geographical location from which the specimens were taken. The range of *scutellaris* is east of the Rocky Mountains while *oregona* occurs in the west limited by the eastern foothills of the Rockies.   Specimens of the subspecies *scutellaris scutellaris* are present in Colorado and New Mexico (Shelford 1917) but these forms are quite different from *oregona* in that they have bright cupreous to red elytra. Another subspecies of *scutellaris*, related to the subspecies *criddlei*, also occurs in Colorado (Rumpp 1961) and it is characterized by broad white margins of the elytra.   The species *depressula* and *oregona*, on the other hand are sympatric.   Individuals of these two species can be told apart by the numbers of hairs forming the clusters near each eye.   The species *oregona* normally has eight to eleven hairs in this area while *depressula* usually has one to three and rarely four.   A more reliable character for distinguishing between *oregona* and *depressula* is the shape of the median lobe of the male.

Like most other species of the *maritima* group *oregona* lives along the edges of rivers, lakes, and sloughs and is found on a variety of substrates. I have taken *oregona* on sandy beaches, gravelly banks, and indeed on rock. This species is more common where there are open patches of beach.

Notes on Synonymy

Casey proposed the names *C. quadripennis* and *C. ovalipennis* for male and female *C. o. oregona* respectively, that occur in Hawthorne, Nevada. Similarly *C. oregona* specimens collected north of San Francisco, were regarded by Casey as a subspecies of *guttifera* and he applied the name *sonoma* to them.   Casey also considered a coastal blue form of *o. oregona* to be a subspecies of *depressula* and named it *scapularis*. However *scapularis* does not itself occur in uniform geographic populations and consequently I have not given it taxonomic status (see Wallis 1961).

Casey's *audax* and *sterope* are both forms of *o. guttifera*.   Their original descriptions indicate these names refer to typical *guttifera* in Colorado and New Mexico. The name *o. oregonella* Casey has been given to specimens from highly variable populations of *o. guttifera* which occur in north central Utah. *C. provensis* Casey refers to blue specimens that were taken in Parowan and Provo Canyon, Utah.   Parowan is located in southwestern Utah, a hybrid area of *o. guttifera* and *o. maricopa*, and Provo Canyon is situated in north central Utah where *o. oregona* and *o. guttifera* intergrade. The name *provensis* represents hybrid individuals of these regions.   Tanner regarded *guttifera* x *maricopa* and *guttifera* x *oregona* hybrid specimens in Utah as being variants of *o. maricopa*.

Geographic Variation and Subspecies

The species *Cicindela oregona* ranges widely in the west, from Alaska to southwestern California, Arizona, and New Mexico and eastward to the Rocky Mountains (fig. 18).   Five easily observed characters vary geographically: body size, color of thoracic pleura, color of elytra, color of pronotum, and expanse of elytral pattern.   Length of elytra is expressed in millimeters from the tip of the scutellum posteriorly to the

tip of the elytral spine along the suture. Width of elytron is similarly expressed in millimeters from the median line of the elytra through the transverse portion of the middle band to the elytral margin. These data are listed in tables 4 and 5 for males and females respectively. The tables also summarize data on variation in diameters of apical dots. The measurements illustrate variation in expanse of the elytral pattern. The apical dot was measured transversely across the widest portion.

Size - Before discussing the geographical aspects of size variation, I would note that females on the average are larger than males of the same population in every locality listed in tables 4, and 5. This is true for the sexes in the same locality, but is not necessarily true if opposite sexes of different regions are compared. For example, females from Trinidad, Colorado have a mean elytral length of 7.23 mm while the average elytral length of males from Tanana River, Alaska is 7.26 mm. Data on variation of elytral length in males and females are given in tables 4 and 5 respectively.

Three geographical routes (A, B, and C in column 1 of tables 4 and 5) have been selected to facilitate description of geographical variation in the length and width of elytra and expanse of color pattern. Tanana River, Alaska and Terrace and Oliver, British Columbia serve as the northern portion for all three routes. The first transect of population samples (A) extends from Alaska, south to New Mexico through British Columbia, Montana, Wyoming and Colorado. A second line of samples (B) is from Alaska to Arizona by way of British Columbia, Idaho and Utah. A third course (C) is from Tanana River, Alaska to southern Nevada, through British Columbia and Idaho. The data in tables 4 and 5 are arranged to correspond to these routes.

Because the corresponding character gradients of males and females are generally parallel, only the male samples are discussed in detail, with occasional reference to female samples. Table 4 indicates a decrease in the mean length of elytra of males, from north to south for all three courses. Each cline is quite irregular and there are sharp decreases and increases throughout. These abrupt changes in the character gradients appear to be correlated, at least in part, with changes in altitude or with geographic barriers. However, I have noted discrepancies in the clines that cannot be so related.

Through the northern section of the first route there is a southward decrease in average length of elytra of 0.007 mm per degree of latitude for males and 0.018 mm per degree of latitude for females. From Alaska to Lower Medicine Lake, Montana a distance of 14°30' of latitude, no marked deviations occur in the trend. Between Lower Medicine Lake and Hardy, Montana however, a distance of only 1°10' latitude, mean length decreases by 0.20 mm. There is a drop of 1,500 feet in altitude between these two localities. Another irregularity in the above character gradient occurs between Helena and Gardiner, Montana - an increase in mean length of elytra of 0.18 mm with 1°30' of latitude. Gardiner is 1,640 feet higher than Helena and contrast in elevation again seems to be related to the clinal difference. Population samples from Gardiner, Montana, Yellowstone National Park, Jackson Hole National Monument, and Moran, Wyoming have elytra of approx-
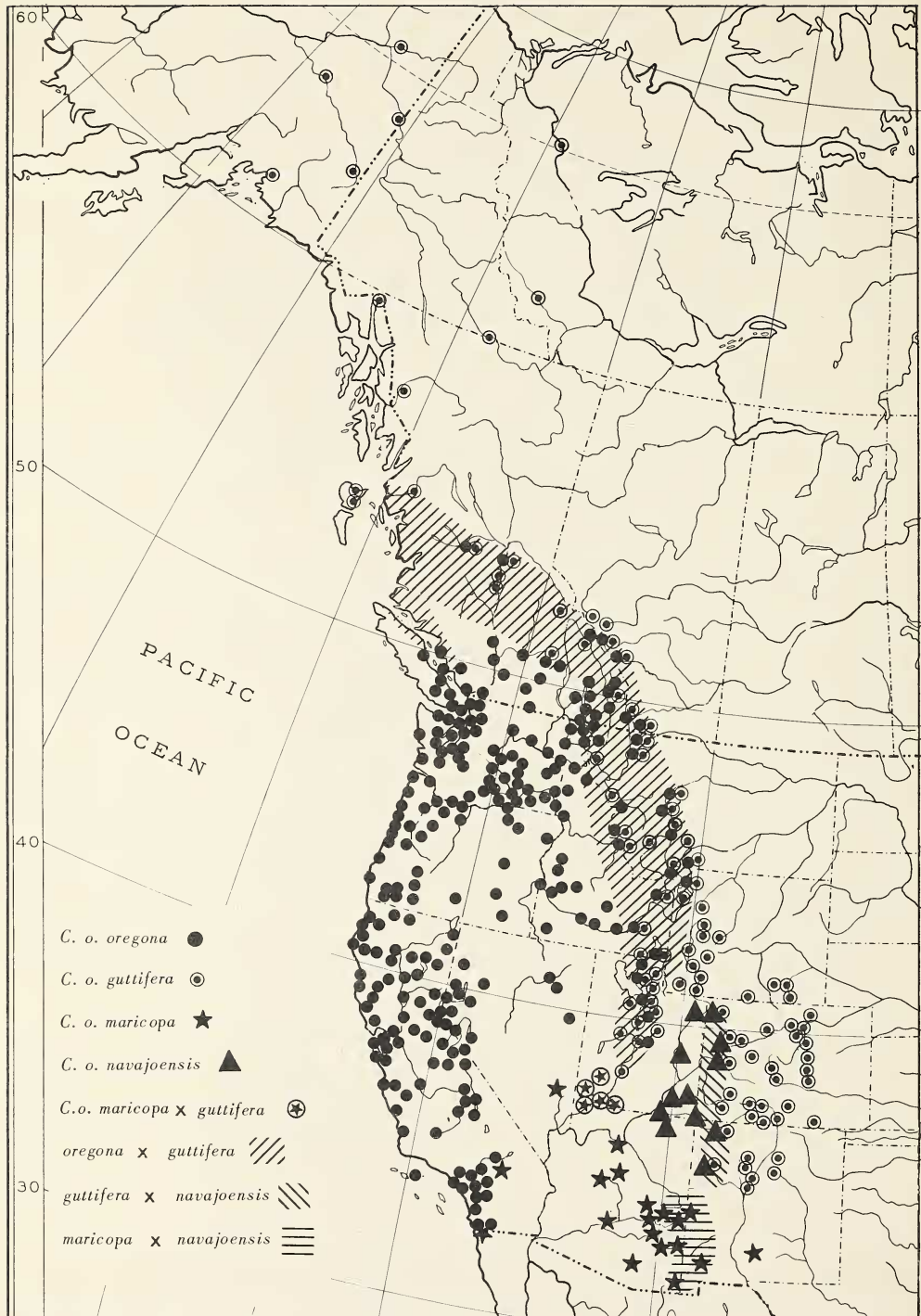
Fig. 18 - Geographical distribution of the subspecies of *C. oregona*.

imately equal length. Immediately southward the slope of the char-
acter gradient decreases markedly between Moran and Labarge,
Wyoming. Both sites are at approximately the same altitude and
there are no obvious geographic barriers between the two localities.
In the Labarge and Green River regions the reduction in body size may
be due to local factors such as disease, lack of food or marginal habitats
(Mayr 1963). Jelm and Saratoga in western Wyoming are rather isolated
from Fort Bridger and Green River, in eastern Wyoming by the Great
Divide Basin and the Continental Divide which are situated in south central
Wyoming. East to west gene flow between populations of *Cicindela oregona* is
most likely impeded in southern Wyoming by these geographical features
which may account for the shorter elytra in eastern Wyoming. The dif-
ference between the average elytral lengths of males from Jelm and Fort
Bridger is statistically significant but that between females is not.

The second arbitrary line of population samples (B) is from Alaska
to Arizona by way of British Columbia, Idaho, and Utah. A clinal de-
crease in length of elytra is evident throughout this route as well. In
Utah, the Alta, Mount Timpanogos, and Provo Canyon populations have
relatively long elytra. The elevation of Alta is 8,585 feet, Mount
Timpanogos is 11,750 feet, and Provo Canyon is located in Provo Park
which rises at a height of 11,068 feet. Samples collected at lower ele-
vations in areas adjacent to the above mentioned, have a shorter mean
elytral length and populations from Stockton and Provo are examples of
these. Population samples taken in Salt Lake City may have been collected
in any of the creeks entering the city from the Wasatch range which serves
as the eastern geographic limits of the metropolis. Although the insects
were labelled as being collected in Salt Lake City, they could conceivably
have been taken at a much higher altitude nearby. Floy, Utah, and Kayenta,
Arizona have populations with the shortest elytra in the entire span of this
gradient. South of Kayenta the samples taken in Prescott, Phoenix, and
Globe, Arizona are larger and compare in size with those from Idaho.
These large forms in central and southern Arizona are fairly isolated and
common only in these areas (see *oregona maricopa* p. 127).

The third line of population samples (C) extends from Alaska, south
through British Columbia and Idaho to Nevada. Even though elytra are
generally shorter in more southerly latitudes, the Walker Lake, Nevada
population sample has the value for mean length of elytra equal to that of
Tanana River, Alaska. I cannot account for this discrepancy.

Data on the variation in width of elytra are presented for males in
table 4 and for females in table 5. There is a slight decrease in width
of the elytra from Alaska, southward along all three routes. Irregularities
in the clines of elytral widths correspond with changes in the character
gradients of the lengths of elytra. At higher elevations of Montana,
Wyoming and Utah mean values for elytral width are generally slightly
greater than those of Alaska and Terrace, British Columbia. Tiger
beetles of this species living in these lower latitudes at high altitudes
are normally shorter but wider than their counterparts in boreal areas.
This is especially marked in females. For example compare population
samples of Tanana River, Alaska, Terrace and Queen Charlotte Islands,
British Columbia with Gardiner, Montana, Alta and Provo Canyon, Utah,

TABLE 4 - Variation in male *Cicindela oregona.*

Length of Elytra

Route	Locality	North lat.	Elev. ft.	N	Range mm	$\overline{X}$ ± SE	SD	CV
A, B, C	Alaska							
	Tanana R.	63.00	1500	16	6.65-7.73	7.26±0.09	0.35	4.75
A, B, C	British Columbia							
	Terrace	54.31	223	19	6.70-7.60	7.24 0.06	0.25	3.49
	Q. Ch. Islands	53.00	0-4100	7	6.81-7.70	7.34 -	-	-
	Oliver	49.10	2143	36	6.35-7.92	7.13 0.06	0.36	5.02
A	Montana							
	Low. Medicine Lake	48.30	5000	44	6.91-7.62	7.16 0.03	0.18	2.49
	Hardy	47.11	3500	17	6.28-7.38	6.96 0.08	0.33	4.80
	Helena	46.35	4160	28	6.61-7.50	7.06 0.05	0.26	3.71
	Gardiner	45.03	5800	40	6.27-7.85	7.24 0.05	0.32	4.36
A	Wyoming							
	Yellowstone Nat. Park	44.30	7000	77	6.13-7.98	7.19 0.04	0.38	5.33
	Jackson Hole Nat. Mon.	43.50	6800	19	6.21-7.79	7.23 0.08	0.34	4.67
	Moran	43.52	6800	27	6.52-8.13	7.22 0.05	0.26	3.57
	11 miles S. Labarge	42.15	6600	16	6.06-7.63	7.01 0.11	0.42	6.05
	27 miles S. Labarge	42.14	6600	14	6.59-7.65	7.03 0.08	0.29	4.18
	Green River	41.33	6100	30	6.13-7.44	6.91 0.07	0.37	5.31
	Fort Bridger	41.19	6657	38	6.46-7.77	7.21 0.05	0.31	4.30
	Saratoga	41.28	6790	15	6.75-7.54	7.09 0.06	0.23	3.23
	Jelm	41.03	7500	46	6.21-7.66	7.01 0.04	0.28	3.95
A	Colorado							
	Estes Park	40.24	7547	12	6.32.7.32	7.02 0.08	0.27	3.85
	Trinidad	37.11	5999	16	6.23-7.03	6.69 0.06	0.25	3.75
A	New Mexico							
	Jemez Springs	35.45	6195	78	6.10-7.45	6.86 0.03	0.29	4.23
	Pecos & Beulah	35.34	7000	10	6.40-7.18	6.73 0.09	0.27	4.01
	Fort Wingate	35.30	6997	13	6.25-7.10	6.66 0.08	0.27	4.05
B, C	Idaho							
	Valley County	45.00	-	7	6.28-7.56	7.01 -	-	-
	Owyhee County	42.30	-	22	6.15-7.61	7.03 0.09	0.40	5.66
	Bear Lake	42.05	5924	61	6.23-7.92	7.02 0.05	0.38	5.34
B	Utah							
	Ogden	41.14	4296	10	6.40-7.75	7.04 0.14	0.43	6.15
	Salt Lake City	40.45	4354	20	6.50-7.73	7.26 0.08	0.35	4.82
	Alta	40.36	8585	2	7.34-7.55	7.45 -	-	-
	Stockton	40.28	5068	11	6.20-7.79	7.00 0.14	0.46	6.54
	Mount Timpanogos	40.24	6000	8	7.00-7.68	7.38 -	-	-
	Provo	40.15	4549	18	6.10-7.62	7.10 0.08	0.36	5.01
	Vineyard	-	-	16	6.20-7.73	7.17 0.10	0.39	5.42
	Provo Canyon	-	5000	12	6.89-7.73	7.25 0.07	0.25	3.48
	Sevier Bridge Reservoir	39.20	5000	11	6.29-7.71	7.04 0.13	0.43	6.07
	Piute Reservoir	38.15	6000	10	6.30-7.43	6.93 0.11	0.34	4.92
	Parowan & Cedar	37.50	5900	17	6.02-7.18	6.79 0.08	0.31	4.59
	Zion N. P.	37.20	4048	6	6.55-7.02	6.78 -	-	-
	Floy	38.56	4000	17	5.75-6.82	6.39 0.08	0.34	5.37
B	Arizona							
	Kayenta	36.44	6300	13	6.90-6.00	6.45 0.08	0.30	4.65
	Prescott	34.34	5280	133	6.00-7.90	7.01 0.03	0.32	4.56
	Phoenix	33.30	1092	11	6.55-7.28	6.85 0.07	0.22	3.21
	Globe	33.23	3541	22	6.50-7.60	7.03 0.06	0.27	3.84
C	Nevada							
	Gerlach & Pyramid Lake	40.40	3900	10	6.40-7.32	6.90 0.11	0.35	5.10
	Reno & Verdi	39.32	4500	10	6.55-7.45	7.07 0.10	0.31	4.40
	Minden	38.58	4600	12	6.58-7.26	6.83 0.06	0.20	2.93
	Hawthorne & Walker Lake	38.31	4326	27	6.57-7.95	7.26 0.07	0.36	5.01
	Caliente	37.36	4407	7	6.00-7.21	**6.57** -	-	-

Width of Elytra				Diameter of Apical Dot			
Range mm	$\overline{X}$ ± SE	SD	CV	Range mm	$\overline{X}$ ± SE	SD	CV
2.45-2.81	2.67 0.03	0.11	3.97	0.42-0.73	0.59 0.02	0.09	14.51
2.50-2.90	2.69 0.02	0.10	3.61	0.35-0.83	0.63 0.03	0.14	21.75
2.52-2.89	2.75 -	-	-	0.50-0.71	0.62 -	-	-
2.36-3.01	2.67 0.02	0.14	5.17	0.45-0.83	0.63 0.01	0.08	13.14
2.52-2.93	2.71 0.01	0.10	3.46	0.34-0.76	0.63 0.01	0.09	14.11
2.30-2.83	2.62 0.03	0.14	5.42	0.40-0.75	0.55 0.02	0.09	15.73
2.49-2.82	2.65 0.02	0.09	3.25	0.39-0.80	0.65 0.02	0.08	12.91
2.30-2.90	2.70 0.02	0.12	4.44	0.43-0.80	0.63 0.01	0.09	14.83
2.34-3.10	2.72 0.02	0.14	5.29	0.28-0.84	0.63 0.01	0.11	16.83
2.40-2.96	2.73 0.03	0.12	4.47	0.50-0.73	0.64 0.02	0.08	12.75
2.49-2.85	2.70 0.02	0.11	4.19	0.41-0.90	0.64 0.02	0.10	15.02
2.31-2.86	2.64 0.04	0.15	5.72	0.52-0.73	0.64 0.02	0.06	9.89
2.54-2.75	2.65 0.02	0.07	2.56	0.44-0.77	0.63 0.02	0.09	14.60
2.31-2.87	2.62 0.03	0.14	5.46	0.40-0.89	0.64 0.02	0.11	16.72
2.42-2.95	2.71 0.02	0.12	4.46	0.40-0.83	0.67 0.02	0.09	14.09
				0.58-0.81	0.68 0.02	0.07	9.63
2.40-2.88	2.67 0.02	0.10	3.86	0.39-0.85	0.67 0.01	0.10	14.93
2.48-2.71	2.62 0.02	0.06	2.29	0.58-0.80	0.69 0.02	0.08	11.45
2.42-2.69	2.58 0.02	0.07	2.83	0.61-0.81	0.70 0.02	0.07	9.71
2.30-2.79	2.60 0.01	0.10	3.85	0.49-0.85	0.71 0.01	0.08	11.00
2.43-2.76	2.60 0.03	0.11	4.23	0.50-0.82	0.67 0.03	0.09	13.43
2.41-2.72	2.56 0.01	0.03	1.17	0.67-0.90	0.78 0.02	0.06	7.69
2.40-2.81	2.64 -	-	-	0.55-0.78	0.65 -	-	-
2.35-2.81	2.62 0.03	0.13	4.85	0.45-0.82	0.62 0.02	0.09	14.08
2.29-2.95	2.66 0.02	0.15	5.60	0.40-0.78	0.61 0.01	0.09	14.66
2.43-2.95	2.68 0.05	0.16	5.97	0.50-0.75	0.65 0.03	0.08	12.55
2.51-2.98	2.76 0.03	0.12	4.38	0.44-0.80	0.64 0.02	0.10	15.62
2.81-2.95	2.88 -	-	-	0.65-0.72	0.69 -	-	-
2.40-2.88	2.70 0.02	0.18	6.81	0.62-0.82	0.72 0.02	0.07	9.81
2.66-2.93	2.83 -	-	-	0.57-0.80	0.69 0.08	-	-
2.50-2.94	2.72 0.03	0.14	5.07	0.60-0.81	0.71 0.02	0.06	9.03
2.39-2.89	2.70 0.03	0.13	4.96	0.50-0.80	0.68 0.02	0.07	10.71
2.64-2.95	2.78 0.02	0.09	3.07	0.55-0.82	0.69 0.02	0.08	11.57
2.43-2.92	2.68 0.05	0.15	5.67	0.50-0.82	0.72 0.03	0.08	11.67
2.50-2.85	2.63 0.04	0.12	4.56	0.55-0.90	0.70 0.04	0.12	16.43
2.35-2.80	2.64 0.03	0.11	4.13	0.55-0.81	0.69 0.02	0.08	11.45
2.50-2.76	2.62 -	-	-	0.58-0.90	0.76 -	-	-
2.20-2.63	2.47 0.03	0.14	5.63	0.66-0.96	0.79 0.02	0.09	11.84
2.20-2.60	2.44 0.03	0.10	4.10	0.62-0.90	0.75 0.02	0.08	10.67
2.20-3.00	2.57 0.01	0.12	4.67	0.55-1.00	0.78 0.01	0.08	10.26
2.25-2.70	2.53 0.04	0.13	5.14	0.61-0.88	0.75 0.02	0.08	10.67
2.30-2.95	2.56 0.03	0.14	5.47	0.65-0.90	0.77 0.01	0.07	9.09
2.44-2.77	2.60 0.04	0.13	4.96	0.62-0.85	0.72 0.02	0.07	10.34
2.40-2.85	2.65 0.05	0.15	1.51	0.60-0.81	0.71 0.02	0.07	9.38
2.35-2.71	2.56 0.03	0.09	3.16	0.50-0.75	0.64 0.02	0.09	13.36
2.56-3.06	2.77 0.03	0.14	5.02	0.52-0.90	0.72 0.02	0.09	13.06
2.25-2.74	2.50 -	-	-	0.55-0.88	0.73 -	-	-

TABLE 5 - Variation in female *Cicindela oregona*.

Length of Elytra

Route	Locality	North lat.	Elev ft.	N	Range mm	$\overline{X}$ ± SE	SD	CV
A, B, C	Alaska							
	Tanana R.	63.00	1500	11	7.65-8.44	7.96±0.08	0.27	3.42
A, B, C	British Columbia							
	Terrace	54.31	223	16	6.56-8.61	7.86 0.12	0.48	6.04
	Q. Ch. Islands	53.00	0-4100	12	7.48-8.51	8.03 0.10	0.33	4.13
	Oliver	49.10	2143	24	6.85-8.57	7.79 0.10	0.48	6.21
A	Montana							
	Low. Medicine Lake	48.30	5000	21	6.95-8.25	7.69 0.08	0.37	4.81
	Hardy	47.11	3500	16	6.56-7.92	7.38 0.09	0.37	5.00
	Helena	46.35	4160	22	7.04-8.32	7.58 0.07	0.32	4.22
	Gardiner	45.03	5800	46	6.90-8.55	7.83 0.06	0.39	4.83
A	Wyoming							
	Yellowstone N.P.	44.30	7000	63	7.10-8.49	7.85 0.04	0.34	4.28
	Jackson Hole N.M.	43.50	6800	8	7.60-8.41	7.91 -	-	-
	Moran	43.52	6800	19	7.42-8.28	7.82 0.06	0.25	3.17
	11 miles S. Labarge	42.15	6600	5	7.55-7.91	7.75 -	-	-
	27 miles S. Labarge	42.14	6600	20	6.72-8.04	7.57 0.09	0.39	5.13
	Green River	41.33	6100	24	6.88-8.12	7.66 0.07	0.34	4.43
	Fort Bridger	41.19	6657	26	7.15-8.21	7.66 0.06	0.31	4.07
	Saratoga	41.28	6790	9	6.46-7.82	7.32 -	-	-
	Jelm	41.03	7500	42	6.80-8.48	7.57 0.06	0.36	4.73
A	Colorado							
	Estes Park	40.24	7547	13	6.98-7.90	7.43 0.08	0.30	3.97
	Trinidad	37.11	5999	10	6.89-7.79	7.23 0.09	0.29	4.05
A	New Mexico							
	Jemez Springs	35.45	6195	85	6.65-8.12	7.47 0.04	0.33	4.42
	Pecos & Beulah	35.34	7000	11	6.83-8.12	7.59 0.11	0.38	5.01
	Fort Wingate	35.30	6997	20	6.50-7.75	7.32 0.07	0.32	4.37
B, C	Idaho							
	Valley County	45.00	-	13	7.00-8.01	7.57 0.09	0.32	4.28
	Owyhee County	42.30	-	40	7.05-8.71	7.80 0.06	0.39	4.97
	Bear Lake	42.05	5924	58	6.45-8.37	7.62 0.06	0.45	5.92
B	Utah							
	Ogden	41.14	4296	3	7.32-7.73	7.59 -	-	-
	Salt Lake City	40.45	4354	21	6.72-8.40	7.71 0.11	0.49	6.41
	Alta	40.36	8585	11	7.34-8.32	7.90 0.09	0.30	3.84
	Stockton	40.28	5068	4	6.71-7.95	7.54 -	-	-
	Mount Timpanogos	40.24	6000	12	7.40-8.25	7.83 0.07	0.24	3.10
	Provo	40.15	4549	18	6.55-8.55	7.72 0.12	0.51	6.59
	Vineyard	-	-	10	7.08-8.31	7.82 0.12	0.38	4.87
	Provo Canyon	-	5000	14	7.10-8.32	7.83 0.08	0.31	3.96
	Sevier Bridge Reservoir	39.20	5000	10	7.12-7.87	7.52 0.09	0.28	3.71
	Piute Reservoir	38.15	6000	8	6.75-8.00	7.51 -	-	-
	Parowan & Cedar	37.50	5900	13	6.53-8.00	7.49 0.12	0.42	5.61
	Zion N.P.	37.20	4048	20	7.00-8.00	7.44 0.07	0.32	4.26
	Floy	38.56	4000	23	5.96-7.52	6.89 0.09	0.43	6.20
B	Arizona							
	Kayenta	36.44	6300	21	6.25-7.85	6.97 0.07	0.36	5.16
	Prescott	34.34	5280	133	6.70-8.50	7.65 0.03	0.38	4.96
	Phoenix	33.30	1092	15	7.10-8.10	7.54 0.09	0.33	4.38
	Globe	33.23	3541	34	6.62-8.10	7.56 0.07	0.40	5.33
C	Nevada							
	Gerlach & Pyramid Lake	40.40	3900	11	7.32-8.20	7.66 0.10	0.33	4.35
	Reno & Verdi	39.32	4500	10	6.24-8.22	7.58 0.21	0.67	8.84
	Minden	38.58	4600	12	7.57-8.10	7.82 0.05	0.18	2.24
	Hawthorne & Walker Lake	38.31	4326	27	6.46-8.60	7.88 0.05	0.49	6.19
	Caliente	37.36	4407	6	6.80-7.72	7.13 -	-	-

Width of Elytra				Diameter of Apical Dot			
Range mm	$\overline{X}$ ± SE	SD	CV	Range mm	$\overline{X}$ ± SE	SD	CV
2.93-3.20	3.08±0.03	0.08	2.71	0.58-0.91	0.73±0.03	0.09	12.98
2.50-3.33	3.07 0.05	0.19	6.22	0.45-0.90	0.72 0.03	0.13	18.33
2.85-3.22	3.08 0.03	0.12	3.90	0.62-0.88	0.76 0.02	0.08	10.50
2.73-3.29	3.07 0.04	0.18	5.93	0.59-0.91	0.74 0.02	0.09	12.59
2.59-3.28	3.02 0.04	0.20	6.49	0.42-0.82	0.68 0.03	0.12	17.21
2.59-3.21	2.93 0.04	0.16	5.43	0.58-0.80	0.68 0.02	0.07	10.04
2.69-3.29	2.98 0.04	0.17	5.57	0.57-0.90	0.72 0.02	0.10	13.89
2.69-3.76	3.09 0.03	0.19	6.18	0.38-0.91	0.74 0.01	0.10	13.70
2.81-3.34	3.10 0.02	0.13	4.32	0.50-0.92	0.76 0.01	0.10	12.62
3.30-3.35	3.16 -	-	-	0.69-0.99	0.81 -	-	-
2.85-3.20	3.07 0.02	0.10	3.26	0.61-0.88	0.75 0.02	0.08	10.43
2.91-3.05	3.02 -	-	-	0.68-0.85	0.74 -	-	-
2.66-3.10	2.95 0.03	0.13	4.34	0.54-0.89	0.71 0.02	0.11	14.79
2.63-3.25	3.01 0.03	0.15	4.95	0.51-0.93	0.74 0.02	0.09	12.59
2.72-3.24	3.02 0.02	0.13	4.14	0.64-1.00	0.80 0.02	0.08	10.60
2.49-3.05	2.84 -	-	-	0.63-0.92	0.78 -	-	-
2.70-3.30	3.00 0.02	0.14	4.53	0.60-0.94	0.78 0.01	0.07	9.18
2.63-3.17	2.88 0.04	0.15	5.10	0.68-0.86	0.77 0.01	0.05	6.49
2.68-3.04	2.86 0.04	0.13	4.51	0.70-0.91	0.81 0.02	0.07	8.27
2.60-3.20	2.94 0.01	0.13	4.42	0.72-1.05	0.87 0.01	0.08	8.25
2.70-3.24	3.00 0.05	0.15	5.00	0.75-1.00	0.88 0.02	0.08	9.09
2.56-3.17	2.95 0.03	0.13	4.41	0.80-1.04	0.92 0.02	0.08	8.70
2.75-3.20	2.98 0.04	0.15	5.03	0.60-0.83	0.72 0.02	0.06	8.00
2.68-3.41	3.07 0.02	0.15	4.66	0.55-1.00	0.77 0.01	0.09	12.12
2.52-3.40	3.01 0.02	0.18	5.87	0.38-1.00	0.74 0.01	0.11	15.41
3.00-3.02	3.01 -	-	-	0.70-0.80	0.73 -	-	-
2.78-3.38	3.08 0.04	0.18	5.97	0.65-0.96	0.79 0.02	0.08	10.62
2.91-3.30	3.14 0.04	0.12	3.76	0.70-1.02	0.80 0.03	0.09	11.19
2.89-3.20	3.09 -	-	-	0.72-0.96	0.88 -	-	-
2.96-3.25	3.13 0.02	0.08	2.55	0.60-0.95	0.83 0.03	0.10	12.53
2.54-3.39	3.07 0.05	0.21	6.91	0.70-0.98	0.86 0.02	0.08	9.77
2.82-3.32	3.09 0.05	0.16	5.28	0.70-0.91	0.81 0.03	0.09	10.90
2.86-3.31	3.09 0.04	0.13	4.30	0.57-0.89	0.76 0.03	0.10	13.16
2.80-3.18	2.95 0.03	0.11	3.76	0.76-0.95	0.84 0.02	0.06	6.87
2.63-3.21	2.95 -	-	-	0.70-0.99	0.84 -	-	-
2.79-3.17	3.00 0.03	0.12	3.83	0.80-0.97	0.86 0.02	0.06	7.50
2.85-3.19	3.01 0.02	0.09	3.14	0.74-1.00	0.87 0.02	0.07	8.33
2.43-3.05	2.77 0.04	0.17	6.14	0.74-1.05	0.91 0.02	0.08	8.77
2.30-2.90	2.66 0.03	0.16	5.83	0.75-1.10	0.89 0.02	0.10	11.24
2.50-3.30	2.93 0.01	0.16	5.51	0.75-1.20	0.93 0.01	0.09	9.68
2.60-3.05	2.84 0.04	0.14	4.93	0.75-1.05	0.90 0.02	0.08	8.89
2.40-3.20	2.85 0.03	0.18	6.32	0.65-1.05	0.90 0.01	0.08	8.89
2.76-3.33	3.04 0.05	0.16	5.30	0.60-0.94	0.78 0.03	0.09	11.47
2.45-3.13	2.94 0.07	0.24	8.06	0.65-0.87	0.79 0.02	0.07	9.48
2.95-3.16	3.06 0.02	0.08	2.61	0.61-0.98	0.79 0.03	0.10	12.03
2.50-3.35	3.10 0.04	0.20	6.39	0.60-1.00	0.84 0.02	0.10	11.67
2.70-2.89	2.82 -	-	-	0.70-0.92	0.81 -	-	-

and Yellowstone National Park, Wyoming in table 5.

        Populations in Nevada are generally longer and wider than samples
from Utah, Colorado, and Wyoming at similar elevations; but east-west
clines are very irregular.

        Specimens collected in Queen Charlotte Islands, British Columbia
are the only insular members recorded in tables 4 and 5. The *oregona* fe-
males of these Islands have a higher mean value for length of elytra than
have those from any other locality listed in table 5, and the mean value
for males is slightly less than those of Alta and Mount Timpanogos, Utah.
However, the male samples from the Queen Charlotte Islands, Mount
Timpanogos, and Alta each are represented by fewer than 10 specimens
and a more accurate comparison can be made with the females. Individuals
from localities of high elevation in Utah, and Wyoming are scarcely
broader than are those of Queen Charlotte Islands (see table 5).

        A relationship of body size with latitude or altitude is evident
in many animal species other than *Cicindela oregona*. North American brown
bears for example, increase in size as the latitude increases (Rausch
1963).   This phenomonon has also been shown in many species of birds
(Mayr 1942, 1963, Hamilton 1961). In insects, honey bees and two species
of European *Carabus* vary in the same way (Mayr 1963, p. 326). New Guinea
dragon flies have been found to increase in size at higher elevations also
(Mayr 1963, p. 326). In ectothermal animals as a whole the largest body
size may just as often be found in the warmest portion of a species
range.   Lindroth (1963) noted that in some Carabids of Newfoundland
dwarf forms are frequently confined to high altitudes or marginal
northern areas of the species range. Ball (1959) observed that several
species of the ground beetle genus *Dicaelus* were larger in southern areas
of their ranges. Likewise the small, flightless grasshopper *Melanoplus puer*
shows a general southward increase in size (Hubbell 1956). Mayr (1963)
presents a review of evidence for the adaptive nature of geographic
variation in which latitudinal and altitudinal changes are discussed in
relation to geographic variation in body size.

        Color pattern of the elytra - While body size of *Cicindela oregona* decreases
from north to south the breadth of the white markings of the elytra in-
creases. The diameter of the apical dot increases approximately 0. 007
mm for each degree of latitude. Data on the expanse of elytral pattern,
illustrated by the diameter of the apical dot, are presented in table 4
for males and in table 5 for females .

        In the first route (A) from Alaska to New Mexico there is a
slight uniform increase in apical dot size through British Columbia and
Montana. In Fort Bridger, Wyoming the cline is steeper and continues to
increase through Colorado to New Mexico. Fort Wingate, New Mexico
is represented by individuals having a very wide apical dot with an average
measurement of 0. 78 mm. The difference between the mean values for
males from Fort Wingate and those from Pecons, New Mexico is stati-
stically significant, but this is not so for females.   The same applies to
material from Hardy,   Montana and from Helena and Lower Medicine
Lake, Montana.

A similar latitudinal increase in the diameter of the apical dot is evident in course (B) from Alaska to Arizona. There is a slight decrease in the mean apical dot size of males in southern Idaho (this is not true for females) but the color pattern expands markedly in Utah. Populations with the widest apical dots are present in Floy, Utah, and Prescott and Globe, Arizona. A similar cline exists in the third path of population samples that extends from Alaska to Nevada.

Coloration - The elytra, thoracic pleura, pronotum and, indeed, the entire body are subject to color variation in this species. The elytra may be brown, green, purple, blue and occasionally very dark brown that is almost black. The thoracic pleura are coppery, metallic blue, purple or green. Color of the pronotum and elytra is generally the same on each individual. Unicolored specimens occur throughout the species range in scattered localities and they are usually green, less frequently blue, In Arizona, southern Nevada, and southern New Mexico a green pronotum is usually associated with purple elytra. North of the limits of populations that have purple elytra the beetles are usually metallic blue-green ventrally and brown dorsally. Figure 19 is a pie-graph map illustrating color variation of the elytra and thoracic pleura in populations in the northern portion of the range of *oregona*. Each "pie" represents a single population sample. Figure 20 is a southwestern continuation of figure 19.

Coppery thoracic pleura are prevalent throughout northwestern British Columbia, Yukon Territory and Alaska. In figure 19 samples A (Tanana River, Alaska) to K (Helena, Montana) coppery thoracic pleura are most frequent, followed in numbers by metallic green, blue and purple, in that order. In Alaska, the Yukon Territory and northern British Columbia, only the coppery condition exists. In samples D, E, F and G, in central British Columbia, individuals with metallic blue-green or purple thoracic pleura are present in low frequency. Southward, coppery thoracic pleura are prevalent in central British Columbia, on the eastern slopes of the Rocky Mountains in Alberta and Montana, and in eastern Idaho, Utah, Wyoming, Colorado, northeastern Arizona and northern New Mexico (see data for Fort Bridger, Wyoming and Jemez Springs, New Mexico in pictorialized scatter diagrams figures 25 and 27). In British Columbia (fig. 19) coppery thoracic pleura are abruptly replaced by metallic purple thoracic pleura and this condition extends throughout southern British Columbia from the Pacific coast east to the Continental Divide. Of the individuals represented in samples L to U, only eight have coppery thoracic pleura in this region. Specimens with metallic green thoracic pleura are common in coastal populations of British Columbia and Washington, and also along the eastern ridge of the Rocky Mountains. This condition is less common in Oregon and California where metallic purple and metallic blue thoracic pleura are dominant (fig. 20). Thoracic pleura of specimens of Owyhee County, Idaho (L) are predominantly metallic purple, also. Populations with thoracic pleura ranging from coppery to metallic purple through metallic blue and metallic green are found in northern Utah near Alta and southern Utah in the area of Zion National Park. Across southwestern United States from San

Diego, California to Mountain Park, New Mexico, specimens with metallic purple thoracic pleura are most frequent.

Brown elytra are most common throughout most of the range of *oregona*. Brown color is entirely replaced by purple color in central Arizona, southern New Mexico and southern Nevada. This situation is discussed in detail in the subspecies section. Populations that are highly variable in color of elytra occur throughout the range of this species. Such populations are on the Pacific coast from Alaska to southern California and almost all individuals with blue or green elytra exist in coastal localities (see figs 19, 20). Brown is most common, followed by green, and then blue. In Garibaldi Park, British Columbia, a very large proportion of specimens with blue elytra are present, while Vancouver and Victoria, British Columbia populations are made up mainly of individuals with green elytra. In Humbolt County, California and Port Orford, Oregon, most of the specimens have brown elytra, and some members with green and blue elytra are also present. Likewise, a few individuals with blue and green elytra are present in San Francisco and in San Diego, California. Variation in elytral color is the rule in northern and southern Utah, where blue, green, and brown specimens are present.

Shelford (1914) studied color and color pattern of tiger beetles and he found, of the species studied in detail, the more brilliant colors occur in warm, arid localities, and extended markings in cooler regions. These findings apply only in part to *oregona*. In Arizona, New Mexico and southern Nevada, which are warm dry areas, specimens with bright metallic dorsal surfaces are prevalent but brilliant blue and green specimens of *oregona* also live along the Pacific coast from California to Alaska, and this is quite a humid zone. The markings of *oregona* are expanded in warmer localities and this condition contrasts with the results obtained by Shelford regarding pattern of elytra.

The pattern of variation - Independent character changes have resulted in discordant variation within *C. oregona*. Elytra are dark brown, generally, in the northern, eastern and western areas of the range but they are purple in the south, and very light brown in eastern Utah. In contrast, pleura usually blue to purple in the west and south, are coppery in northern and eastern portions of the range. In addition general body size decreases clinally from the north to south and also varies from higher to lower altitudes. Finally extent of white markings on elytra increases southward. Although recognition of subspecies in species that show discordant variation is controversial, (p. 90 , and Inger 1961) I think it is useful to group into subspecies the population samples of *oregona*.

Maintenance of variation in this species appears to be largely dependent on geographical factors but may also be due to variation in the season of occurrence of adults. Mature specimens of my own and other collectors from boreal populations appear to be most plentiful for June, July, and August (based on specimen label information and personal collecting). This seems to be true for alpine populations in southern regions as well. Adult specimens from populations in desert areas of Utah, Arizona, and New Mexico have been collected from March to October inclusive. This suggests that they are common throughout this time but
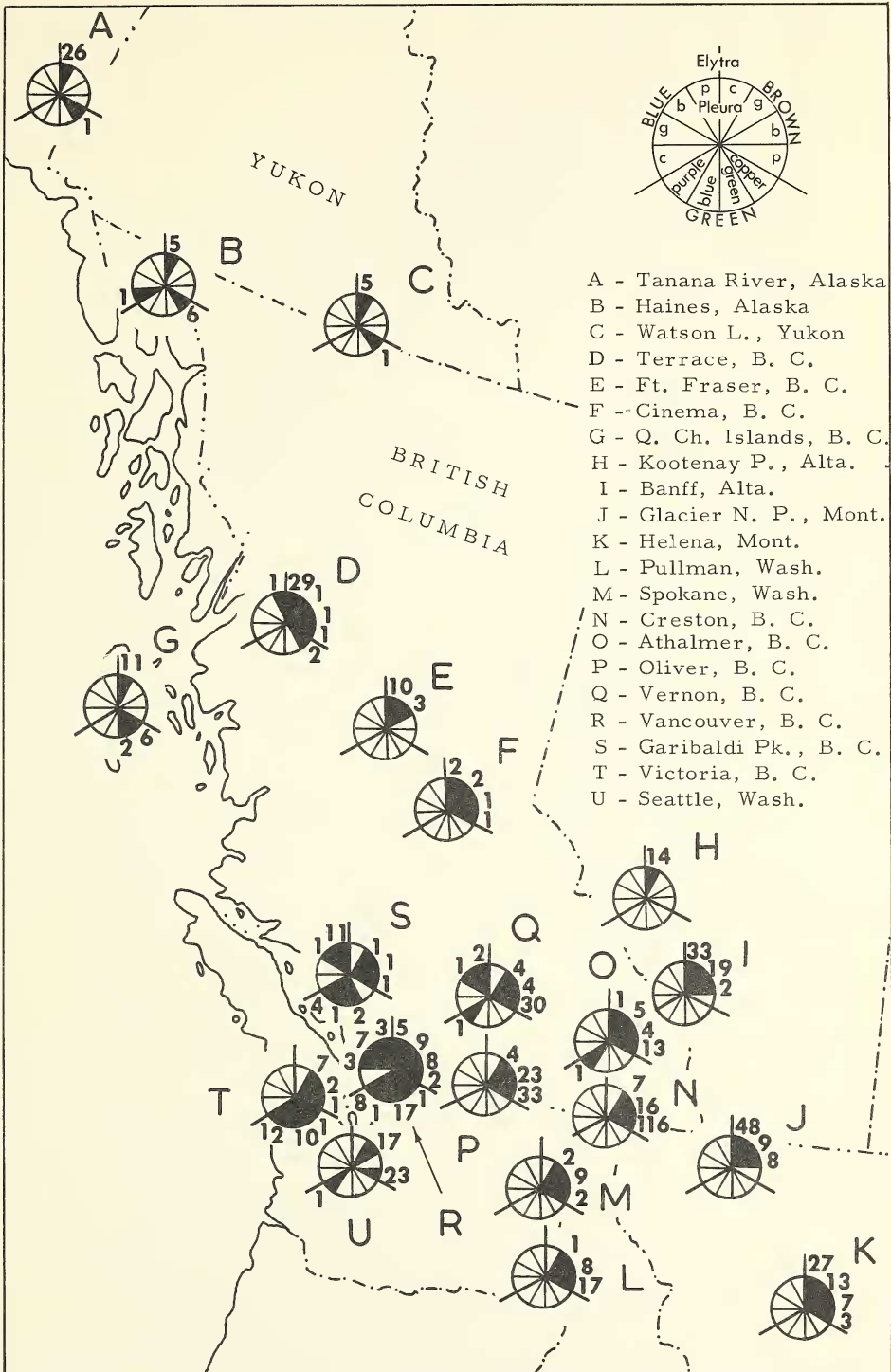
Fig. 19. Pie-graph map illustrating geographic variation in the color of the elytra and thoracic pleura of some populations samples of *Cicindela oregona* . The numbers of specimens with a given color combination are indicated opposite the appropriate section. Thus, 20 placed at 1 o'clock signifies that 20 specimens have coppery thoracic pleura and brown elytra.
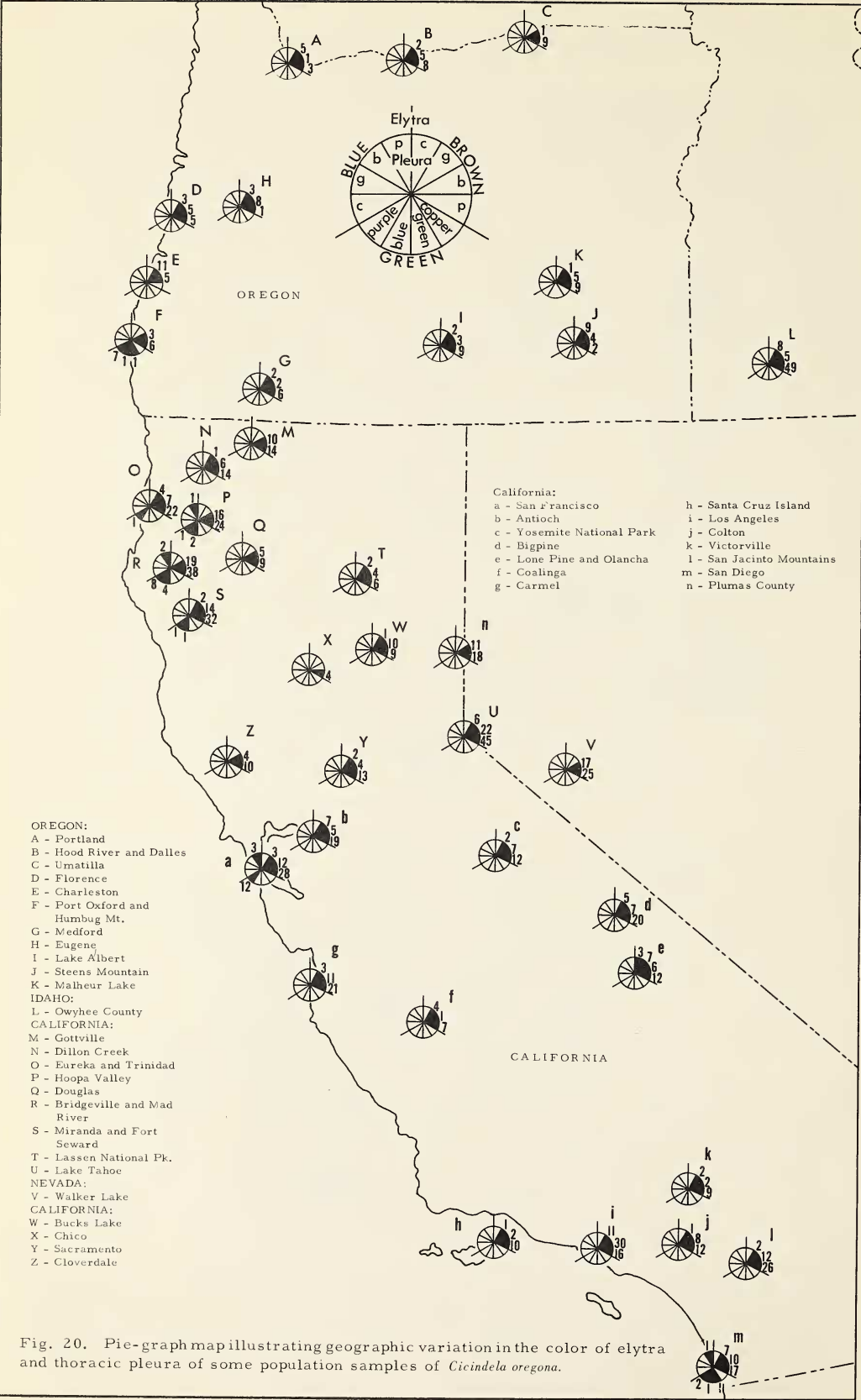
Fig. 20. Pie-graph map illustrating geographic variation in the color of elytra and thoracic pleura of some population samples of *Cicindela oregona*.

I do not believe so. Because *C. oregona* is riparian, size of populations, in arid southwestern regions, is likely to fluctuate with rain. Kendrew (1961) points out that rainfall is variable in these desert regions with a max- imum in late summer and winter, and that the mountain ranges which rise on the southwestern plateau have rather more rain. It follows that activity peaks of desert populations probably do not occur at the same time year after year but in different periods in relation to rainfall. Attempts to col- lect desert forms during winter months have been unsuccessful. Perhaps they are most numerous during late summer-later than the peak of alpine populations.   Such asynchronous number fluctuations effect a reduction in gene flow and thus maintain the variation between desert and alpine populations of the southwest.

   Subspecies - I recognize four subspecies of *Cicindela oregona*. I have followed the 75% rule in defining the group taxonomically (see p. 90 , and Mayr *et al.* 1953). The differences between two or more populations in two or more characters are best illustrated by a pictorialized scatter diagram. Ten such diagrams and a locality map of the population samples compared in the scatter diagrams are presented as figs 21-31. Subspecies can be readily distinguished from each other on the basis of one or more exter- nal characters.   Males and females are treated separately.   Generally five localities are represented in each diagram.   Each locality is re- presented by ten specimens or less, and they have been selected randomly. Fifty specimen symbols are placed on a diagram.

1   Thoracic pleura blue or purple............................ 2
         Thoracic pleura coppery.................................. 3
2   Elytra purple, elytral pattern broad, pronotum green........
         .... *o. maricopa*
         Elytra brown, green, blue, or rarely purple; elytral
         pattern narrow; pronotum brown..................... *o. oregona*
3   Elytra light brown; elytral pattern broad........... *o. navajoensis*
         Elytra dark brown; elytral pattern narrow............ *o. guttifera*

   The nominate subspecies *Cicindela oregona oregona* ranges from south- ern British Columbia in Canada,   to southwestern California. it is present throughout Washington, Oregon, and California, except for the southeast portion of that state.   The Continental Divide serves as the eastern limit in the north, from Banff, Alberta south to Yellowstone National Park, Wyoming.   Further south *oregona oregona* is found as far east as Owyhee Count, Idaho, western Nevada and finally near the south- ern portions of the Sierra Nevada Mountains in California (fig. 18). A combination of green, blue, or brown elytra with metallic purple or blue thoracic pleura is characteristic of this subspecies. Individuals with green elytra are numerous in or near the above localities.   The scattered occurrence of these blue and green individuals along the Pacific coast may be evidence of a blue form that was once widespread in these

coastal regions, but was infiltrated by a more vigorous stock, character-
ized by the possession of brown elytra. Whenever these two aggregates
of populations came into contact introgression took place and the presence
of green individuals interpreted as hybrids, marks what once were zones
of contact. In more southern locations these green and blue forms have
been all but completely replaced by brown. On the other hand they may
be recent phenotypes whose gene complex originated in southwestern
British Columbia when the blue phenotypes were relatively common.
Another possibility is that the green and blue forms might be ecopheno-
types. Although Shelford observed that *Cicindela tranquebarica* Herbst is
green on the coasts and coastal mountains and also that in *Cicindela scutellaris*
green forms were most common along the Atlantic coast (Shelford 1917),
he did not believe that this was the result of direct influence of the en-
vironment on the phenotypes.

The subspecies *o. oregona* comes in contact with *o. guttifera* LeConte
in southern British Columbia and along the slopes of the Rocky Mountains
from Banff, Alberta to Yellowstone National Park, Wyoming. Many
specimens that appear to be hybrids are present in areas of contact of
these two subspecies, and such are distinguished by their metallic
green thoracic pleura (fig. 19).

In San Diego, California a hightly variable group of populations
is present (fig. 20), for in this area specimens typical of both *o. oregona*
and *o. maricopa* occur. This situation could be the result of *maricopa* genes
infiltrating the more numerous *oregona* population in the region (figs 22,
23). Only five phenotypically *maricopa* specimens are known from the San
Diego area.

Cicindela o. guttifera ranges the Rockies from Fort Yukon, Alaska to
northern New Mexico (fig. 18). In Alaska and north and central British
Columbia, *guttifera* ranges from the Pacific coast to the eastern slopes of
the Rockies but continues southward in a very narrow zone to northern
New Mexico. This subspecies also occurs in northern and central Utah.
Coppery thoracic pleura and brown elytra that have a metallic lustre
characterize it. I have already mentioned that hybridization takes place
between *oregona guttifera* and *oregona oregona* in much of eastern Idaho and
western Montana, and intermediate specimens with metallic green sides
are not uncommon in northern and central Utah where they are distributed
through *oregona guttifera* populations. In southwestern Utah a highly variable
series of populations occurs, consisting of individuals ranging from typ-
ical *guttifera* to typical *maricopa* . This region is undoubtedly a melting pot
of these two subspecies (figs. 24, 25). It may be argued that this var-
iation is a result of hybridization between *oregona* and *maricopa* and not as
above. This is not likely since at the present time *oregona* is uncommon in
eastern Nevada and it is not abundant in Utah, but it may have contributed
to this variation in pluvial times.

The ranges of *Cicindela o. navajoensis* and *guttifera* come very close in
northwestern New Mexico (fig. 18). *Navajoensis* is relatively small in size
and has much lighter brown elytra and broader pattern of elytra than
guttifera. Like the latter, *navajoensis* has coppery thoracic pleura. A
color character gradient occurs from Kayenta, Arizona to Jemez Springs,
New Mexico through an intermediate locality, Fort Wingate, New Mexico.

Color of the elytra in Kayenta is light brown, dark brown in Jemez Springs and intermediate in Fort Wingate. Fort Wingate specimens are also intermediate in lengths and widths of elytra and the apical dot (figs 26, 27).
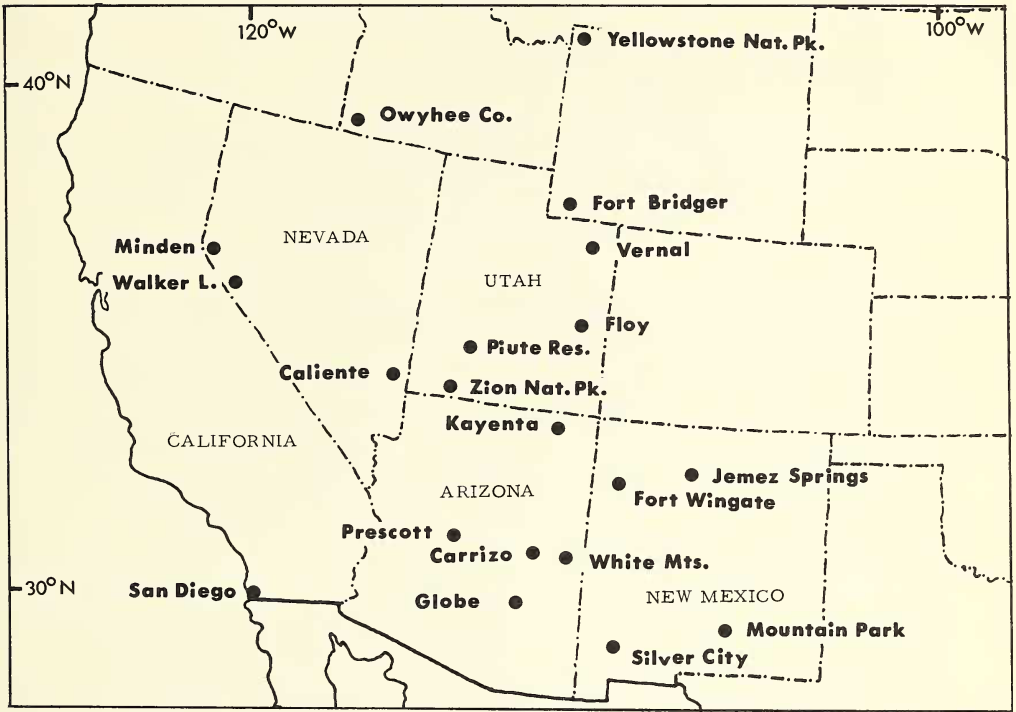

Fig. 21 - Locality map of population s a m p l e s of *C. oregona* LeConte compared in scatter diagrams.

The geographic ranges of *oregona* and *navajoensis* are not in contact; their morphological relationships are demonstrated in figs 28 and 29.

In southeastern Arizona and southwestern New Mexico are variable populations that consist of individuals structurally between *navajoensis* and *maricopa* (figs 30, 31). The members of these groups are generally smaller in body size than *maricopa* and larger than *navajoensis*. Their elytra are mainly purplish brown. The Fort Wingate sample in figures 30 and 31 is not pure *navajoensis* but is intermediate between *navajoensis* and *guttifera* (figs 26, 27). Thus the specimens appear as intermediates between *navajoensis* and *maricopa* in figures 30 and 31.

Specimens of *o. maricopa* have brilliant purple elytra, brown to metallic green pronota, and metallic purple thoracic pleura. *Maricopa* is distributed sparsely through southern California, southeastern Nevada, and southern New Mexico, but it is common in central and southern Arizona (fig. 18). California "*maricopa*" may be a minor element in predominantly *o. oregona* populations and if so they are *maricopa* in a typological sense only. The form of this and other subspecies of *Cicindela oregona* has been compared
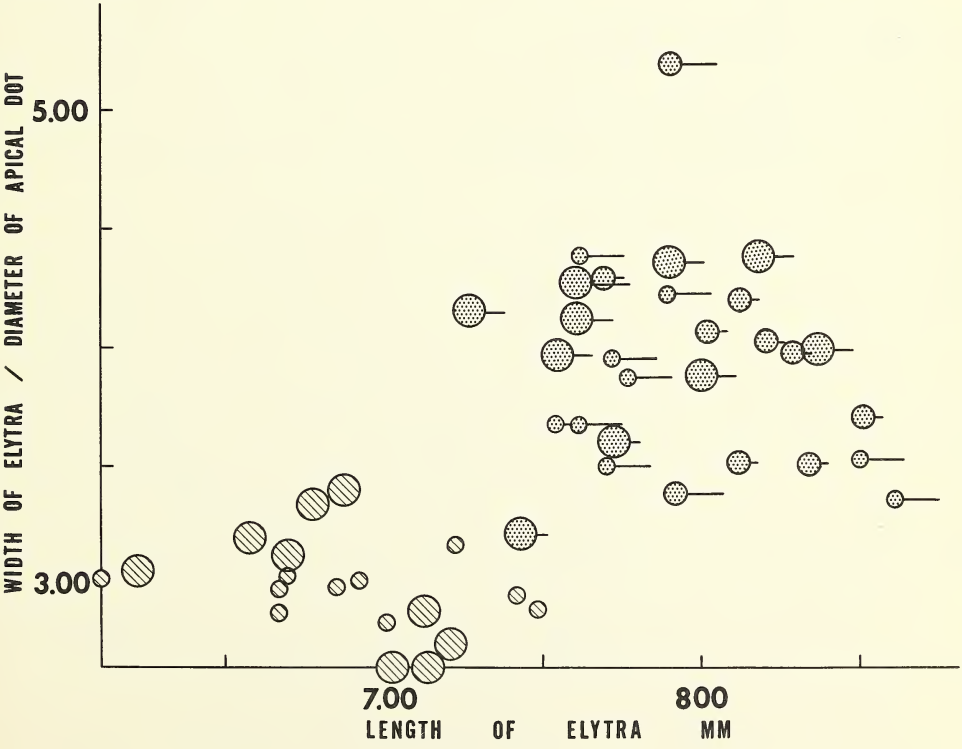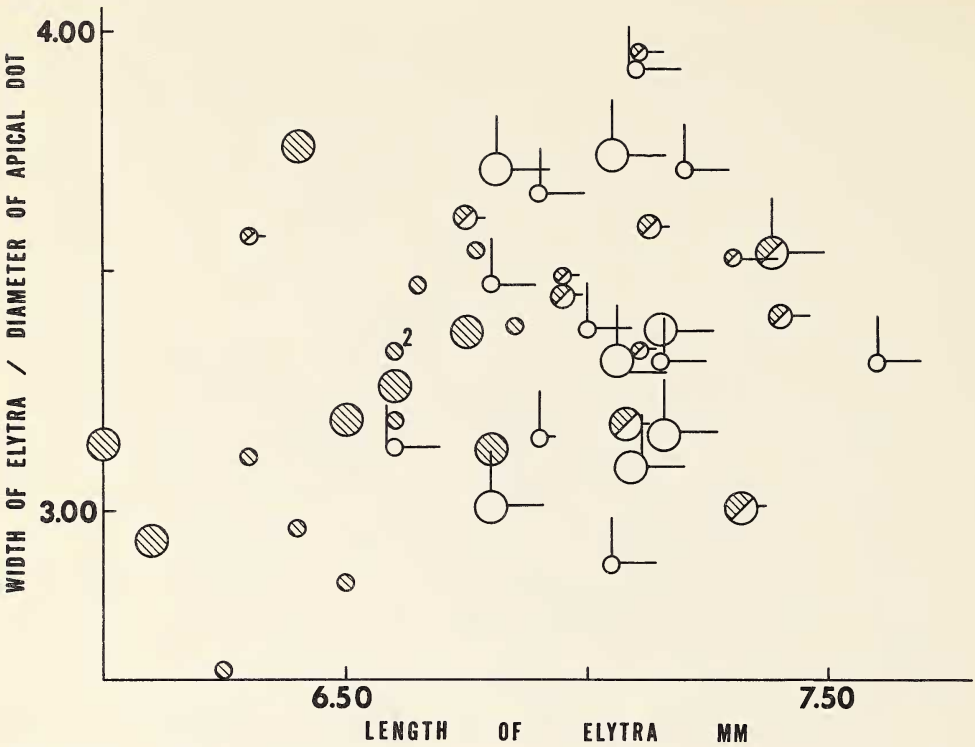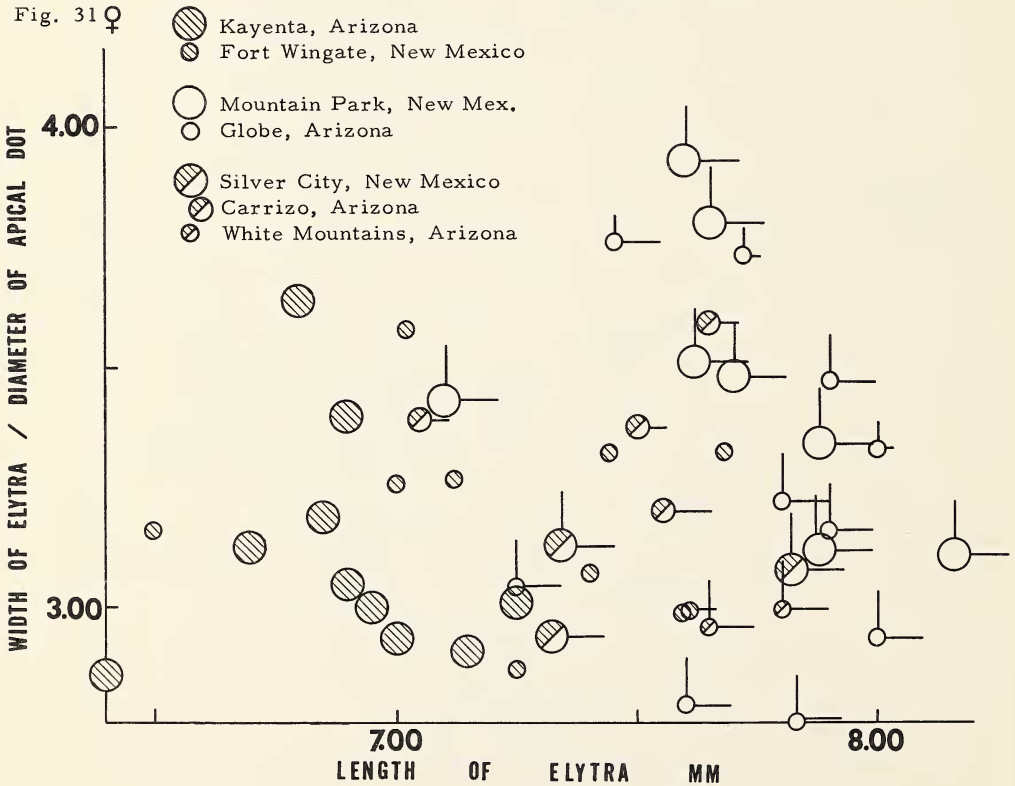
128

Figs. 22 to 31. Pictorialized scatter diagrams illustrating character differences between population samples of *C. oregona oregona* (⊚), *C.o. maricopa* (○), *C.o. guttifera* (●), and *C.o. navajoensis* (⊗). Intermediate populations represented by divided circles (⊘) (●) (⊗) (⊘); elytral color by vertical bars: long - purple, medium - green, short - blue, no bar - brown; pleural color by horizontal bars: long- purple, medium - green, short - blue, no bar - coppery. Males above, females below.

Fig. 24 ♂

Fort Bridger, Wyoming
Piute Reservoir, Utah

Caliente, Nevada
Prescott, Arizona

Zion Nat. Pk., Utah

WIDTH OF ELYTRA / DIAMETER OF APICAL DOT

5.00

3.00

6.50   7.50

LENGTH   OF   ELYTRA   MM

Fig. 25 ♀

WIDTH OF ELYTRA / DIAMETER OF APICAL DOT

4.00

3.00

7.00   8.00

LENGTH   OF   ELYTRA   MM

130

Fig. 26 ♂

Vernal, Utah
Jemez Springs, New Mexico
Kayenta, Arizona
Floy, Utah
Fort Wingate, New Mexico

WIDTH OF ELYTRA / DIAMETER OF APICAL DOT

4.00

3.00

6.00   LENGTH   OF   ELYTRA   MM   7.00

Fig. 27 ♀

WIDTH OF ELYTRA / DIAMETER OF APICAL DOT

4.00

3.00

7.00   LENGTH   OF   ELYTRA   MM   8.00

Figs. 22 to 31. Pictorialized scatter diagrams illustrating character differences between population samples of *C. oregona oregona* (⊖), *C.o. maricopa* (◯), *C.o. guttifera* (●), and *C.o. navajoensis* (⊘). Intermediate populations represented by divided circles (⊘ ◐ ◑ ⊘); elytral color by vertical bars: long - purple, medium - green, short - blue, no bar - brown; pleural color by horizontal bars: long- purple, medium - green, short - blue, no bar - coppery. Males above, females below.

Fig. 28 ♂

Yellowstone Nat. Pk.,
Wyoming
Walker Lake, Nevada
Owyhee Co., Idaho

Kayenta, Arizona
Floy, Utah

WIDTH OF ELYTRA / DIAMETER OF APICAL DOT

5.00

3.00

6.00   7.00   8.00

LENGTH   OF   ELYTRA   MM

Fig. 29 ♀

WIDTH OF ELYTRA / DIAMETER OF APICAL DOT

5.00

3.00

7.00   800

LENGTH   OF   ELYTRA   MM

Figs. 22 to 31. Pictorialized scatter diagrams illustrating character differences between population samples of *C. oregona oregona* (⊘), *C.o. maricopa* (○), *C.o. guttifera* (●), and *C.o. navajoensis* (⊗). Intermediate populations represented by divided circles (⊘ ◐ ◕ ⊘); elytral color by vertical bars: long - purple, medium - green, short - blue, no bar - brown; pleural color by horizontal bars: long - purple, medium - green, short - blue, no bar - coppery. Males above, females below.

above.

History of Distribution and Subspeciation

Distribution of *C. oregona* is restricted to western United States and Canada bounded by Alaska, southern California, Arizona and New Mexico and the Rocky Mountains. Within this area four geographically distinct groups of populations exhibit boundaries that are generally barriers such as deserts and mountain ranges (fig. 18). All population samples of these subspecies that I have examined, have been collected in the above described range of *C. oregona*. I have seen two *maricopa* specimens, however, that are labelled "Texas", but specific localities are not given. They could have been collected in western Texas near *maricopa* localities in New Mexico. Because the total range of *C. oregona* is well marked and no populations occur in remote regions outside of the described range it appears highly likely that subspeciation took place somewhere in western North America.

Before discussing further the questions of how and when formation of subspecies occurred in *oregona* it should be emphasized that determination of evolution of a subspecies without a fossil record is a highly speculative matter. Fossils are not available, and even if they were it would be impossible to determine all of the subspecific development in *oregona* because color is rarely preserved in fossils. As a result indirect evidence must be used. This is provided by a consideration of the effects Pleistocene climatic changes may have had on bringing about subspeciation in *oregona*.

It seems that isolation of groups of populations of *oregona* occurred at different times in relation to climatic changes. In southern portions of the species range populations were separated from each other during interglacial periods because of the formation of deserts. Northern incipient subspecies were probably separated during glacial times.

Because *oregona* is riparian, regions void of river systems and lakes act as geographic barriers. The great deserts of southwestern United States prove to be barriers (fig. 18), and distribution of subspecies is closely linked to wet and cool areas. Consequently it may be deduced that isolation and subsequent genetic divergence of southern populations took place when southwestern United States was largely desert; perhaps during the last interglacial period. During glacial times, on the other hand, river systems were very extensive and many lakes occurred in the southwest (Blackwelder 1948, Hubbs and Miller 1948). In these regions populations were undoubtedly dispersed most widely in glacial times and presumably gene flow was uninhibited.

Conversely, partitioning of incipient subspecies that existed in northern regions of this species range probably occurred during glacial times, while range expansions occurred in interglacial periods. In glacial periods great ice masses moved down from the north, scarcely crossing the Canadian-American border in the west. These undoubtedly obstructed gene flow between aggregates of populations on the eastern portions of the Rockies and populations further west by way of northern United States and southern Canada. For example if an ice mass was at

present established across the northwest *o. oregona* and *o. guttifera* would be spatially isolated because they normally intergrade in Idaho, Montana, southern Canada and northern Utah. Similarly glaciers that developed throughout most of the major mountain ranges in glacial times must have reduced east-west gene flow further south.

Interpretation of present distribution of the subspecies and knowl-edge of the events of the Pleistocene epoch suggests the following course of subspeciation (see fig. 32). Two subspecies of *C. oregona, oregona* and *guttifera* as they are defined here, were formed in part during the Iowan glacial stage. A uniform "protooregona" species was distributed across northwestern United States and southwestern Canada prior to this period. With the advent of the Iowan ice mass and glacier formation all "proto-oregona" populations north of the Canadian - American border were probably annihilated, at least as a result of cooling and, two large pop-ulations were isolated, one on either side of the Continental Divide; race A on the west and race B on the east. Both races were more wide-spread in the south than they now are. Race B occupied all of the Great Basin, Arizona and regions west of the Sierra Nevada. Geographic variation was pronounced in this race with brown forms predominant in the north and blue in the south. Restricted to regions east of the Con-tinental Divide in the north, race A extended southward into Colorado and New Mexico then swung northward through lower elevations in northwest-ern New Mexico and northeastern Arizona and eastern Utah. This was the situation when the Prairie interglacial stage began.

Much division and spatial isolation between southern populations took place during the Prairie interglacial as a result of vast desert form-ation. During this stage southern, blue populations of race B subspeciated to *maricopa* and brown western (race B) populations to *oregona*. Race A forms became *navajoensis* and *guttifera*. Distributions of aggregates of populations shrank and assumed geographic areas approximately where the subspecies of *C. oregona* now exist. *C. oregona* blue populations in the south were pinched off from their counterparts in the northwest by deserts where the Mohave Desert and Great Basin are now located. In Utah *navajoensis* populations remained partially isolated from populations in Colorado by the intervening Rocky Mountains, and were isolated from the effects of the *oregona* blue forms in the southwest. In the north *oregona* and *guttifera* reinvaded regions south of the retreating ice mass in northern United States and Canada and formed marked hybrid areas wherever their ranges came into contact.

Southern hybrid zones were primarily formed in the Wisconsin glacial period as a result of expanding subspecific ranges. Pluvial lakes that were reestablished in desert areas along with revived river systems served as routes for expanding ranges and intergradation was widespread. In the north *oregona* and *guttifera* were isolated from each other as in the previous glacial period.

Since the Wisconsin ice age ranges of subspecies have shrunk in the southwest. A few specimens phenotypically *maricopa* have been found in southern California but true *maricopa* is abundant only in central Arizona. This implies that *maricopa* once was more extensively distributed. On the other hand *oregona* and *guttifera* ranges appear to be expanding in the north.

Furthermore distribution of hybrids in the southwest has recently been
reduced in area.   Evidence of this is available in southeastern Arizona
and southwestern New Mexico.   Pure *maricopa* specimens   along   with
maricopa x   *navajoensis* hybrids exist in these regions, but pure populations
of *navajoensis* are located in northeastern Arizona and northwestern   New
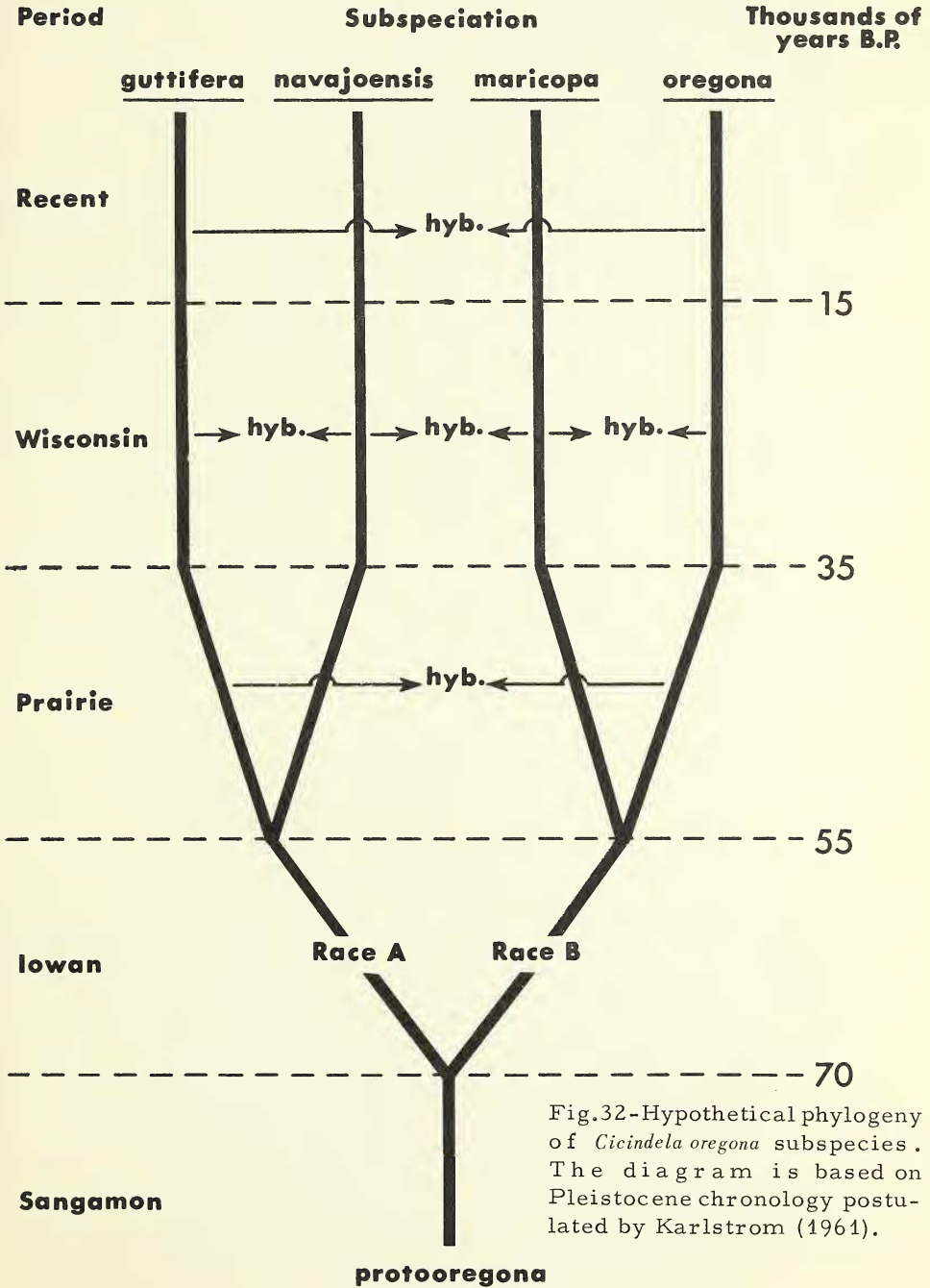Mexico, many miles away from where the hybrids are found.

Fig.32-Hypothetical phylogeny
of *Cicindela oregona* subspecies.
The diagram is based on
Pleistocene chronology postu-
lated by Karlstrom (1961).

Cicindela duodecimguttata and *C. o. guttifera* may have formed hybrid populations along the southeastern foothills of the Rocky Mountains during Pleistocene times. Such hybrid populations were probably subject to extreme fluctuations as in Nordegg, Alberta at the present time (p. 156). These unstable intermediate forms had no profound effect on the parental forms.

This discussion presents one interpretation of subspeciation in *C. oregona* that is based on knowledge of distribution pattern of *C. oregona* and Pleistocene events in southwestern United States. Undoubtedly other explanations of the available data are possible.

Distribution

I examined 6,073 specimens. Several specimens appeared to be labelled wrongly. Two *maricopa* specimens were labelled Fort Garland, Castilla County, Colorado. Fort Garland is well into *guttifera* territory beyond the northern limits of *maricopa* at that longitude. Another *maricopa* specimen is labelled Sonoma County, California, which is in northwestern California approximately seven hundred miles north of the *maricopa* specimens in San Diego. Five specimens of *o. guttifera* were labelled as being collected in Santa Rita Mountains. This is unlikely but not impossible since these specimens could represent a relict population which has survived in these mountains since the end of the Pleistocene.

Cicindela oregona oregona LeConte. Canada. BRITISH COLUMBIA:
Abbotsford, 9; Agassiz, 25; Ainsworth, 6; Aiyansh, 1; Atbara, 7; Bear Foot, 1; Cherrierville, 2; Chilliwack, 2; Columbia Lake, 1; Comox, 8; Copper Mine, 2; Courtenay, 4; Cranbrook, 3; Creston, 139; Duncan, 3; Duncan and Cowichan Lake, 1; Elk Lake, 1; Fairmont, 1; Field, 1; Fraser River, 1; Gabriola, 2; Garibaldi Park, 29; Golden, 1; Goldstream, 1; Harrison, 2; Hatzic, 20; Hope, 1; Howser, 7; Huntingdon, 15; Kamloops, 3; Kaslo, 8; Keremeas, 2; Likely, 1; Lillooet, 9; Lynn Valley, 1; Lytton, 2; Mabel Lake, 2; MacGillivray, 53; McIntyre Creek, 1; Merritt, 22; Miracle Beach, 60; Misson City, 20; Nanaimo, 1; Nanoose, 5; North Bend, 4; Okanagan Lake, 1; Oliver, 61; Osoyoos, 2; Peachland, 3; Pender Harbour, 5; Penticton, 3; Point Grey, 2; Powell River, 2; Radium, 3; Read Bay, 4; Riondel, 11; Rock Creek, 7; Salmon Arm, 3; Sanca, 12; Shuswap Falls, 1; Stillwater, 1; Summerland, 4; Tood Inlet, 1; Trinity, 1; Vancouver, 79; Vancouver Island, 5; Vaseaux Lake, 13; Vernon, 42; Victoria, 18; White Lake, 2; Windemere, 1; Wynndel, 8.
United States. CALIFORNIA: Alameda County: 11; Berkley, 17; Oakland, 10. Alpine County: 7; Soda Springs, 1. Butte County: Chico, 4; Chico Creek, 1; Oroville, 2. Calaveras County: Big Trees, 6; Mokelumne Hill, 7. Contra Costa County: Antioch, 12; Del Norte County: Crescent City, 6; Terwah, 1. Eldorado County: Bijou, 2; Desolation Valley, 1; Echo, 1; Fallen Leaf Lake, 1. Fresno County: Cedar Grove, 1; Coalinga, 12; Fresno, 3; Huntington Lake, 15; Macy Mines, 1; Stevenson Creek, 1. Glenn County: Elk Creek, 2. Humbolt County: Blue Lake, 2; Blairs Ranch, 3; Bridgeville, 28; Bridgeville (15 miles east), 5; Eel River, 1; Eureka, 9; Ferndale, 2; Fort Seward, 26; Hoopa, 44; Miranda, 29; Pepperwood, 1; Jct. Redwood Creek and Rte. 299, 12; Scotia, 3; Trinidad, 1; Trinidad (5 miles south), 25; Van Duzen River, 2; Willow Creek, 1. Inyo County: Bigpine (2 miles west), 12; Bigpine (2 miles north), 20; Biship, 2; Lone Pine, 11; Olancha, 18; Owens Lake, 1. Kern County: Bakersfield, 2; Bakersfield (4 miles east), 9; Cottonwood Creek, 1; Isabella, 1. Lake County: Borax Lake, 5; Hullville, 3; Lake Pillsbury, 8; Lakeport, 2; Lower Lake, 1. Lassen County: Facht, 1; Goumaz, 4; Madeline, 1; Pine Creek, 1; Susanville, 1. Los Angeles County: Burbank, 2; Covina, 1; Crystal Lake, 1; El Monte, 3; Gabriel Mountains, 1; Los Angeles, 57; Palmdale, 1; Point San Pedro, 1; San Pedro, 1; Santa Monica, 10; Tropico, 1. Madera County: Jackass Meadow, 1; Madera, 1; North Fork, 2; Placer Station, 2. Marin County: Bon Tempe, 4; Dillon Beach, 6; Inverness, 1; Lagunitas, 1; Mill Valley, 1; Point Reyes Station, 4. Mariposa County: Mariposa Grove, 1; Yosemite National Park, 22; Yosemite Valley, 1. Mendocino County: Caspar, 1; Eagles Nest, 1; Fort Bragg, 1; Littleriver, 2; Philo, 1; Yorkville, 3. Merced County: Lake Merced, 7; Los Bonos, 1; Santa Rita, 2. Modoc County: Cedarville, 2; Goose Lake, 1; Lake City, 1. Mono County: Coleville, 1; Lake Mary, 5; Mono Lake, 13; Mono Lake, 6; Sonora Pass, 2; Topaz Lake, 8. Monterey County: Bradley, 1; Carmel, 34; Pacific Grove, 1; Salinas River, 6; Soledad, 2; Stone Canyon, 4. Nevada County: Norden, 2; Soda Springs, 1; Truckee, 7. Orange County: Anaheim, 5; Laguna Beach, 2. Placer County: Brockway, 2; Dutch Flat, 2; Lake Tahoe, 75; Summit, 1. Plumas County: Bucks Ranch, 20; Clio, 1; Meadow Valley, 1; Near Twain, 1; Quincy (4 miles west), 2; Tobin, 1; U.S. Alt. 40 (2.1 miles W., U.S. 395), 30; Walker Mine, 1. Riverside County: Hemet Res., 8; Idyllwild, 20; Indio (30 miles north), 2; Lake Elsinore, 2; Riverside, 12; San Jacinto Mountains, 13; Temecula, 1; White Water Canyon, 2. Sacramento County: Sacramento, 19. San Bernadino County: Big Bear, 7; Big Bear Valley, 1; Cajon, 3; Cajon Pass, 1; Colton, 21; Victorville, 13; Yermo, 1. San Diego County: Descanso, 1; Guatay, 1; Julian, 3; Mesa Grande, 5; Oceanside, 1; Poway, 1; Warner Springs, 1. San Francisco County: San Francisco, 22. San Joaquin County: Stockton, 7. San Luis Obispo County: Paso Robles, 1; Pismo Beach, 3. San Mateo County: Salada Beach, 7. Santa Clara County: Los Gatos, 1; Palo Alto, 2; San Jose, 3. Santa Cruz County: Santa Cruz, 4; Soquel Basin, 3. Santa Cruz Island, 13. Shasta County: Bumpas Hell, 1; Lassen National Park, 5; Castella, 2; Hat Creek, 3; Hat Lake, 1; Manzanita Lake, 4; Mount Lassen, 3; Redding, 3; Shasta National Forest, 3; Shasta Springs, 11; Viola, 1. Sierra County: Sierraville, 9; Viola Pass, 1. Siskiyou County: Dillon Creek, Klamath River Valley, 21; Dunsmuir, 4; Gottville, Klamath River Valley, 24; Etna, 3; McCloud, 10; Tule Indian Reservation, 1. Solano County: Dixon, 1. Sonoma County: Cloverdale, 15; Duncans Mills, 1; Santa Rosa, 4. Stanislaus County: Patterson, 1. Sutter County: Yuba City, 5. Tehama County: San Bernardino Mountains, 1. Trinity County: Douglas City, 14; Jct. Mad River, Rt. 36, 37. Tulare County: Burton Meadow, 1; Kaweah, 2; Lemoncove, 6; Lloyd Meadow, 1; Sequoia National Park, 8. Tuolumne County: Hardin Flat, 12; Pinecrest, 1; Strawberry Resort, 11. Yolo County: Davis, 6. Localities of unknown counties: Alta, 1; Asilomar, 1; Bear Lake, 1; Bentons Crossing, 3; Big Dalton Dam, 6; Borego, 1; Bryson 1; Carrville, 14; Charity Valley, 1; China Flat, 2; Colony Mill, 1; Ebbet Pass, 1; El Mirador, 1; Fort Ross, 3; Giant Forest, 2; Hackamore, 5; Hartsooks, 2; Hickey Grove, 7; Hueneme, 1; Ingleside, 2; Kings River, 11; Lake Clay, 1; Lassen Creek, 1; Leech Lake Mountain, 6; Marble Bridge, 1; Marwedel, 1; Miami, 1; Mount Tallac, 1; Panoche Canyon, 1; Paradise Springs, 1; Pohono, 3; Poloa, 4; Poso Creek, 1; Redstone, 2; Sandflat, 6; San Juan, 1; San Pedro Valley, 15; Shaver, 1; Sheep Creek, 1; Silliman, 1; Simmler, 1; Sylvania, 1; Tassajara, 5; Towie, 1; Tunnel R.S., 1; Vera Lake, 1; Waddell Beach, 2; Walker, 6. IDAHO: Ada County: 4; Boise, 2. Blaine County: Carey, 1. Boise County: 13. Bonner County: Hope, 1; Priest Lake, 1; Priest River, 5; Sandpoint, 1. Boundary County: Selway Falls (2.5 miles south), 1. Canyon County: 8; Nampa, 1. Elmore County: Atlanta, 2. Gooding County: Hagerman, 1. Idaho County: 4. Jerome County: Jerome, 1. Kootenai County: Cataldo, 1; Coeur d'Alene, 5; Medimont, 1. Latah County: Moscow, 7; Troy, 1. Nez Perce County: Lake Lowell, 2; Lewiston, 5. Owyhee County: Homedale, 1; Owyhee County, 62. Power County: American Falls, 1. Shoshone County: Wallace, 1. Valley County: Cascade, 1; McCall, 1. Valley County: 20. NEVADA:

Churchill County: Fallon, 3. Douglas County: Lake Tahoe, 1; Minden, 24. Elko County: Elko, 4; Lamoille, 1. Mineral County: Hawthorne, 10; Walker Lake, 45. Ormsby County: Carson City, 3. Pershing County: Lovelock, 1. Washoe County: Gerlach, 2; Mount Rose, 1; Nixon, 1; Pyramid Lake, 18; Reno, 19; Verdi, 1. White Pine County: McGill, 1. OREGON: Baker County: Pine Creek, 1; Richland, 1. Benton County: Corvallis, 8; Umatilla, 10. Clackamas County: Estacada, 4. Clatsop County: Cannon Beach, 1; Clatsop Beach, 2. Columbia County: Rainier, 1. Coos County: Cape Arago, 2; Charleston, 16; Coos Bay, 4; Coos Head, 1. Curry County: Humbug Mountain, 6; Port Orford, 12. Grant County: John Day George, 2. Harney County: Frenchglen, 8; Malheur Lake, 15; P. Ranch, 1; Steens Mountains, 15. Hood River County: Hood River, 8; Mount Hood, 2; Parkdale, 1. Jackson County: Medford, 10; Rogue River, 1; Ruch, 2. Josephine County: Grants Pass, 5; Hells Gate Bridge, 2; Murphy, 1. Klamath County: Crater Lake, 2; Klamath Lake, 6; Lake O Woods, 3; Pinehurst (21.9 miles east), 1. Lake County: Lake Albert, 12; Paisley, 3. Lane County: Eugene, 13; Florence (3 miles north), 13. Lincoln County: Depoe Bay, 2; Newport, 6; Waldport, 5; Yachats (5 miles south), 5. Linn County: Cascadia, 1. Malheur County: Sucker Creek Canyon, 1. Marion County: Detroit, 1. Multnomah County: Portland, 9. Tillamook County: Pacific City, 1; Tillamook, 1; Woods, 4. Umatilla County: Echo, 2; Hermiston, 3; Meadow Lake, 1. Wasco County: The Dalles, 7; Tygh Valley, 1. Yamhill County: Dayton, 6; McMinnville, 4. Localities of unknown counties: Alvord Hot Springs, 3; Blitzen Valley, 1; Boiler Bay, 5; Buell, 1; Devils Lake, 1; Durnep, 2; McNair Lake, 1; Moffat Mead, 1; Ocean Park, 1; Oregon (south east), 3; Santiam, 4; Sparks Lake, 1; Whitman, 2. UTAH: Salt Lake County: Alta, 13; Brighton, 1. Utah County: American Fork Canyon, 9. WASHINGTON: Adams County: Othello, 7. Asotin County: Asotin, 1; Clarkston, 1. Benton County: Paterson, 1. Chelan County: Leavenworth, 1; Peshastin, 4; Stehekin, 1; Wenatchee, 5. Clallam County: Port Angeles, 1. Columbia County: Huntsville, 3. Douglas County: Moses Coulee, 3. Franklin County: Kahlotus, 2; Pasco, 1. Grant County: Beverly, 3; Goose Lake, 1; Moses Lake, 1; Stratford, 9. Grays Harbor County: Moclips, 3. Island County: Coupeville, 1; Whidby Island, 53. Jefferson County: Port Townsend, 17. King County: Auburn, 2; Bothell, 4; Cedar Mountain, 5; Maple Valley, 3; Renton, 13; Seattle, 80; Selleck, 1; Snoqualmie, 1. Kitsap County: Bremerton, 49; Chico, 34; Gorst, 120; Keyport, 1; Kingston, 13; Manchester, 1. Kittitas County: Ellensburg, 2; Vantage, 12. Klickitat County: Goldendale, 1; Goldendale (32.3 miles north), 22. Lewis County: Chehalis, 2. Lincoln County: Sprague, 2. Mason County: Lake Cushman, 1; Spillman, 2. Okanogan County: Brewater, 5. Pacific County: Bay Center, 4; Ilwaco, 1; Long Beach, 1; Nahcotta, 2; North Cove, 1; Ocean Park, 3. Pend Oreille County: Newport, 1. Pierce County: Buckley, 1; Chinook Pass, 3; Mount Rainier, 1; Summer, 1; Tacoma, 4. San Juan County: False Bay, 1; Friday Harbor, 9. Skagit County: Anacortes, 18. Snohomish County: Cicero, 2; Darrington, 6; Everett, 3; Index, 4; Sulton, 1; Verlot, 8. Spokane County: Medical Lake, 4; Spokane, 13. Stevens County: Wellpinit, 1. Thurston County: Olympia, 1; Tenino, 5. Walla Walla County: Dixie, 10; Lowden, 1; Touchet, 27; Wallula Gap, 1. Whatcom County: Bellingham, 1; Mount Baker, 2. Whitman County: Almota, 3; Pullman, 30; Wawawai, 11. Yakima County: Toppenish, 4; White Swan, 1; Yakima, 2. Localities of unknown counties: Barkerville, 1; Blue Mountains, 1; Central Ferry, 1; Clifton, 1; Ginko State Park, 2; Half Moon Lake, 2; Lyone Ferry, 9; Neppel, 10; Paha, 5; Pot Holes, 2; Saratoga Beach, 5; Silverton, 1; Skating Lake, 1; Stillaguamish, 2; Tolsak, 1.

Cicindela oregona guttifera LeConte. Canada. ALBERTA:
Kootenay Plains, 14. BRITISH COLUMBIA: Aiyansh, 1; Blue River, 1; Bucks Bar, 1; Cariboo Road (mile 185), 2; Glenora, 1; McNab Creek, 1; Juskalta, 6; Massett, Queen Charlotte Islands, 10; Moresby Camp, Queen Charlotte Islands, 9; Queen Charlotte City, 1; Stickeen River, 1; Tlell, Queen Charlotte Islands, 9. NORTHWEST TERRITORIES: Fort Good Hope, 2; South Nahanni River, 1. YUKON TERRITORY: Kirkman Creek, 1; Watson Lake, 6.

United States. ALASKA: Eagle, 3; Fairbanks, 5; Fort Yukon, 11; Haines, 12; Tanana River, 27; Valdez, 4; Yukon River, 1. COLORADO: Alamosa County: Alamosa, 3. Boulder County: Boulder, 5; Jamestown, 2; Lyons, 1; Pinecliffe, 2. Chaffee County: Buena Vista, 2; Salida, 3. Clear Creek County: Georgetown, 1. Conejos County: Cumbres Pass, 4; La Manga Pass, 4. Douglas County: Larkspur, 2. El Paso County: Cascade, 1; Colorado Springs, 6; Colorado Springs (10 miles south), 6; El Paso County: 2; Manitou Springs, 5. Freemont County: Coalcreek, 1. Garfield County: Glenwood Springs, 1. Grand County: Big Muddy Creek, 1; Fraser, 1. Jefferson County: Golden, 7. La Plata County: Electra Lake, 1. Larimer County: Estes Park, 25; Fort Collins, 1. Las Animas County: Trinidad, 26. Mineral County: Creede, 4; Wolf Fall Creeks, 2. Ouray County: Ouray, 1. Park County: Colorado Springs (50 miles west), 4. Pitkin County: Aspen, 4. Saquache County: Great Sand Dunes National Monument, 4. Teller County: Victor, 1. Localities of unknown counties: Berkley, 1; Gothic, 1; Rockwood, 2; South Fork, 1; Thomasville, 1. NEW MEXICO: Bernalillo County: Albuquerque, 1. San' Doval County: Bernalillo, 1; Jemez Mountains, 17; Jemez Springs, 47; Jemez Springs (9 miles north), 73; Jemez Springs (10 miles north), 43. San Miguel County: Beulah, 2. Santa Fe County: Pecos River, 17; Santa Fe (3 miles east), 2. Localities of unknown counties: San Antone, 1. UTAH: Beaver County: Beaver Creek, 1. Cache County: Logan, 3. Juab County: Levan (5 miles south), 1. Millard County: Lynndyl, 1. Piute County: Piute Reservoir, 18. Rich County: Bear Lake, 1. Salt Lake County: Mount Dell Creek, 1; Parley Canyon, 3; Salt Lake City, 18; Salt Lake County, 24. Sampete County: Sevier Bridge Reservoir, 21. Summit County: Echo, 2; Park City, 3. Tooele County: Stockton, 15. Uintah County: Power Plant, 2. Utah County: Mount Timpanogos, 20; Payson, 1; Provo, 17; Provo Canyon, 26; Utah Lake, 19. Wasatch County: Soldier Summit, 3; Wasatch County, 2. Weber County: Ogden, 13; Ogden (30 miles east), 8. Localities of unknown counties: Emigration, 1; Hillneck Canyon, 1; Kawara, 6; Red Butte Canyon, 1; Salt Creek Canyon, 1; Silver Lake, 5; Vineyard, 26. WYOMING: Albany County: Centennial, 1; Jelm, 88. Carbon County: Baggs, 2; Saratoga (8 miles south), 24. Fremont County: Lander, 1. Lincoln County: Labarge (11 miles south), 21. Sublette County: Big Sandy Reservoir, 11; Half Moon Lake, 11; Sweetwater River, 2. Sweetwater County: Green River, 54; Green River (26 miles south), 6; Old Ford on Green River, 34; Sweetwater County, 7. Uinta County: Fort Bridger, 64; Lyman, 4.

Cicindela oregona maricopa Leng. United States. ARIZONA:
Coconino County: Grand Canyon, 1. Gila County: Globe, 56; Roosevelt Lake, 4; San Carlos, 1; Sierra Ancha Mountains, 7. Graham County: Rylas, 8. Greenlee County: Clifton, 9. Maricopa County: Phoenix 25 ; Tempe, 1. Pima County: Tuscon, 5. Pinal County: Pinal Mountains, 7. Yavapai County: Cottonwood, 1; Haslampa, 3; Prescott, 266. Localities of unknown counties: Bad Creek Canyon, 1; Bradshaw Mountains, 1; Mogollon Mountain, 1; Oak Creek Canyon, 2. CALIFORNIA: Los Angeles County, 1. San Bernardino County: Barstow, 1. NEVADA: Lincoln County: Caliente, 13; Meadow Valley, 1. NEW MEXICO: Otero County: Cloudcroft, 2; Mountain Park, 15. UTAH: Iron County: Cedar City Canyon, 2.

Cicindela oregona navajoensis Van Dyke. United States.
ARIZONA: Navajo County: Betatakin, 9; Kayenta, 25; Navajo Mountain, 6. Moffat County: Echo Park, 2; Massadona, 4. Montezuma County: Four Corners, 4. UTAH: Grand County: Floy, 40; San Juan County: Blanding (10 miles west), 4; National Monument, 1; Navajo Mountain Trading Post, 7.

Cicindela oregona oregona x *Cicindela oregona guttifera*

Canada. ALBERTA: Banff, 52; Laggan (Lake Louise), 22; Waterton Park, 5. BRITISH COLUMBIA: Athalmer 24; Canal Flats, 8; Cinema, 7; Fernie, 25; Fort Fraser, 13; Kootenay National Park, 6; Moyie, 2; Terrace 35; Wasa, 7; Yoho National Park, 17.

United States. IDAHO: Bannock County: Pocatello, 7. Bear Lake County: Bear Lake, 119. Bloomington Lake, 10. Franklin County: Franklin Basin, 11. Fremont County: Parker, 2. Lemhi County Salmon (21 miles north), 6. MONTANA: Cascade County: Great Falls, 2. Flathead County: Hungary Horse 11; Kalispell, 1. Gallatin County: Bozeman, 2; Gallatin County, 2; Gallatin River and Highway 10, 14;   Lak Hebgen, 12; Missouri River (headwaters), 2; Three Forks (3 miles west), 13. Glacier County: Lower Medicin Lake, 66. Lewis and Clark County: Craig, 14; Helena, 50; Hardy (15 miles south west), 33. Lincoln County Troy, 1. Missoula County: Frenchtown, 2. Park County: Gardiner (5 miles north), 86. Ravalli County: Darby, 2; Florence, 2; Hamilton, 3; Ravalli County, 2; River Bottoms, 10; Skalkaho, 1. Sanders County: Whitepine, 1. Silver Bow County: Butte, 1. Localities of unknown counties: Beaver Creek, 8; Bitter Root Mountains, 2; Lost Horse Canyon, 1; Marias River, 2; Stickney Creek, 34. WYOMING: Teton County: Black Rock Creek, 4; Grand Teton National Park, 13; Hobach Canyon, 3; Jackson Hole National Monument, 27; Moran (38 miles east), 46. Yellowstone National Park, 140.

Cicindela oregona oregona x *Cicindela oregona maricopa.*

United States. CALIFORNIA: San Diego County: San Diego, 45.

Cicindela oregona guttifera. x *Cicindela oregona maricopa.*

United States. UTAH: Beaver County: Beaver (4 miles east), 11; Beaver Canyon, 6; North Creek, 1. Iro: County: Burkshire, 1; Cedar City, 9; Iron Springs, 2; Parowan (5 miles south east), 7; Parowan Canyon, 12. Kane County: Glendale, 1; Kanab, 1; Orderville, 2. Washington County: Bellvue, 2; Pine Valley, 2; Pintura 3; Saint George, 8; Santa Clara, 3; Zion National Park, 26. Localities of unknown counties: Mount Meadows 1; Weeping Rock, 1.

Cicindela oregona guttifera x *Cicindela oregona navajoensis.*

United States. COLORADO: Mesa County: De Beque, 4; Palisade, 7. NEW MEXICO: McKinley County Fort Wingate, 33. San Juan County: Farmington, 3. UTAH: Uintah County: Dinosaur National Monument 1; Vernal, 12.

Cicindela oregona navajoensis x *Cicindela oregona maricopa.*

United States. ARIZONA: Apache County: White Mountains, 8. Cochise County: Chiricahua Mountains, 2. Navajo County: Carrizo, 8; Cibeque Creek, 2. NEW MEXICO: Catron County: Luna, 5. Brant County Silver City, 6.

The Species *Cicindela depressula* Casey.

Cicindela depressula depressula Casey 1897:297. Type locality - Placer County, California. Leng 1902:150. Rivalier 1954:253.

> *Cicindela oregona depressula* Hatch (not Casey 1897) 1953:42. Horn 1930:82. Wallis 1961:24.

Cicindela depressula eureka Fall 1901. Type locality - Humbolt County, California. NEW COMBINATION.

> *Cicindela eureka* Fall 1901:307. Leng 1902:149. Horn 1930:82. Rivalier 1954:253.

Two constant differences set apart *depressula* from other species of the *maritima* group. First, in *depressula* two or three hairs usually occupy the small area near the front inner edge of each eye; four hairs are seldom present. If these hairs are abraded, setigerous punctures indicate their former positions. Second, the distal end of the median lobe of the male genitalia of *depressula* has two distinct, broad flanges that form a blunt apex (for details see fig. 3, and p. 91). A partially diagnostic character   is the form of the middle band of the elytra. In Oregon and California the middle band of *depressula* tapers evenly posteriorly. This contrasts with the sharp bend in the middle band of *oregona*. On the other hand in Washington, Canada, and Alaska the middle band of *depressula* often appears identical with that of *oregona*.

I collected *oregona* and *depressula eureka* on the same sand bank along the Van Duzen River near Bridgeville, California; and Ball (personal communication) collected *d. depressula* and *o. guttifera* in the same area at Terrace, British Columbia, and at Haines, Alaska. There was no evidence of hybridization or cross-mating at these locations, and this suggests that *depressula* and *oregona* are specifically distinct in spite of their many shared characteristics.

Notes on Synonymy

The tiger beetles called *depressula* and *eureka* are very similar to one another, differing mainly in color and markings of the elytra and in seasonal occurrence of adults. They are also allopatric. The differences, however, are not absolute; that is, range of variation in the diagnostic characters of the two forms is slightly overlapping. Furthermore, Rumpp has from the Olympic National Forest, Washington, a series of specimens interpreted as hybrids between *depressula* and *eureka*. These considerations of variation and distribution suggest that *depressula* and *eureka* are conspecific, but are subspecifically distinct. Rumpp and I have reached this conclusion independently.

Geographic Variation and Subspecies

Eleven population samples, whose geographic positions collectively span the known range of this species were selected on the basis of geographical location and number of specimens and were examined for variation. Elytral size, elytral color, pleural color, and the condition of the middle band vary. There maybe a humeral dot on the elytra. Variation in these was analyzed and the results are summarized in tables 6-8.

Length of elytra was examined in a cursory fashion (table 6). Mean values for females are higher than those for males from the same locality. Mean values for samples from lowland, coastal regions in Humbolt County, California are normally higher than mean values for populations from Mount Rainier, Washington. This is the reverse of the pattern of the size variation in *oregona*.

TABLE 6 - Variation in length of elytra of male and female *d. depressula* and *d. eureka*.

	Sex	N	Range mm	$\overline{X}$ ± SE	SD	CU
d. depressula	male	25	6.62-8.07	7.25 0.07	0.35	4.85
	female	25	6.70-8.42	7.60 0.08	0.38	5.00
d. eureka	male	25	6.72-8.12	7.51 0.06	0.32	4.21
	female	25	7.35-9.03	8.31 0.08	0.42	5.02

Populations of the Cascade Range differ in phenology from those of the Pacific coast of Oregon and California. At these latitudes populations from these regions do not meet, for apparently there is a difference in seasonal occurrence of adults. Most adults in alpine regions are active during the middle and late summer but in coastal populations the adults are out earlier in the year. On a collecting trip in June 1963 *depressula* was not found at high elevations, but specimens of

coastal populations were collected in northwestern California.

Elytra of *depressula* have a metallic lustre and are either brown, green or blue (table 7). There is no evidence of a uniform character gradient. Brown elytra are prevalent in coastal regions of northern California, on Mount Hood, Oregon and on Mount Rainier, Washington. Specimens with green elytra occur throughout the range of the species , but are most frequent at both northern and southern extremities of the range, e. g. Haines, Alaska and Eldorado County, California. Blue elytra are most common in populations from Washington and southern British Columbia and as such parallel those of *oregona* in southwestern British Columbia. In California, over 90 per cent of specimens from Cascade Range localities are green whereas over 90 per cent from the coast are brown.

Color of thoracic pleura is rather variable in every population listed in table 7 except for Lassen National Park and Eldorado County, California. Specimens with green and coppery thoracic pleura are more common than those with blue.

Data on variation in the humeral dot are presented in table 8. The humeral dot is present in all specimens collected in lowland localities near the Pacific coast. Among specimens from localities in the Cascade Mountains, the dot may be present or absent. Over 90 per cent of the specimens from north of and including Mount Baker, Washington have humeral dots on the elytra, but only 10 per cent of the specimens from southern Oregon and California have them. In the Mount Rainier, Washington and Mount Hood, Oregon samples the two conditions occur in about equal frequencies. The variation appears to be clinal.

The middle band of the elytra may be broken or complete, and the data on the frequencies of these conditions in various population samples are presented in table 8. In general the broken condition of the middle band is more common southward, among montane populations, but this is a poorly marked trend. All of the specimens from coastal regions in California have a complete middle band.

Variation in hair between the eyes is not tabulated. However, between the eyes, in the middle of the head, one to four very fine hairs are present in coastal specimens' from southern localities. The hairs rarely appear on specimens from northern montane regions, or on specimens from montane localities in California. These hairs should not be mistaken for the setae near the front inner edge of the eyes that are characteristic of *depressula* as a whole.

Most northern populations studied exhibit appreciable variation. The five specimens from Haines, Alaska are less variable but more material is necessary from northern localities to obtain a better knowledge of the degree of variation. In the central portions of the range, variation is discordant. Southern populations, however, are remarkably uniform.

Of the characters considered above, specimens collected in southern areas of the Cascade Range vary mainly in the condition of the middle band. Almost all of these specimens have the elytra and thoracic pleura green, and no humeral dot. These characters are generally most common in northern populations.
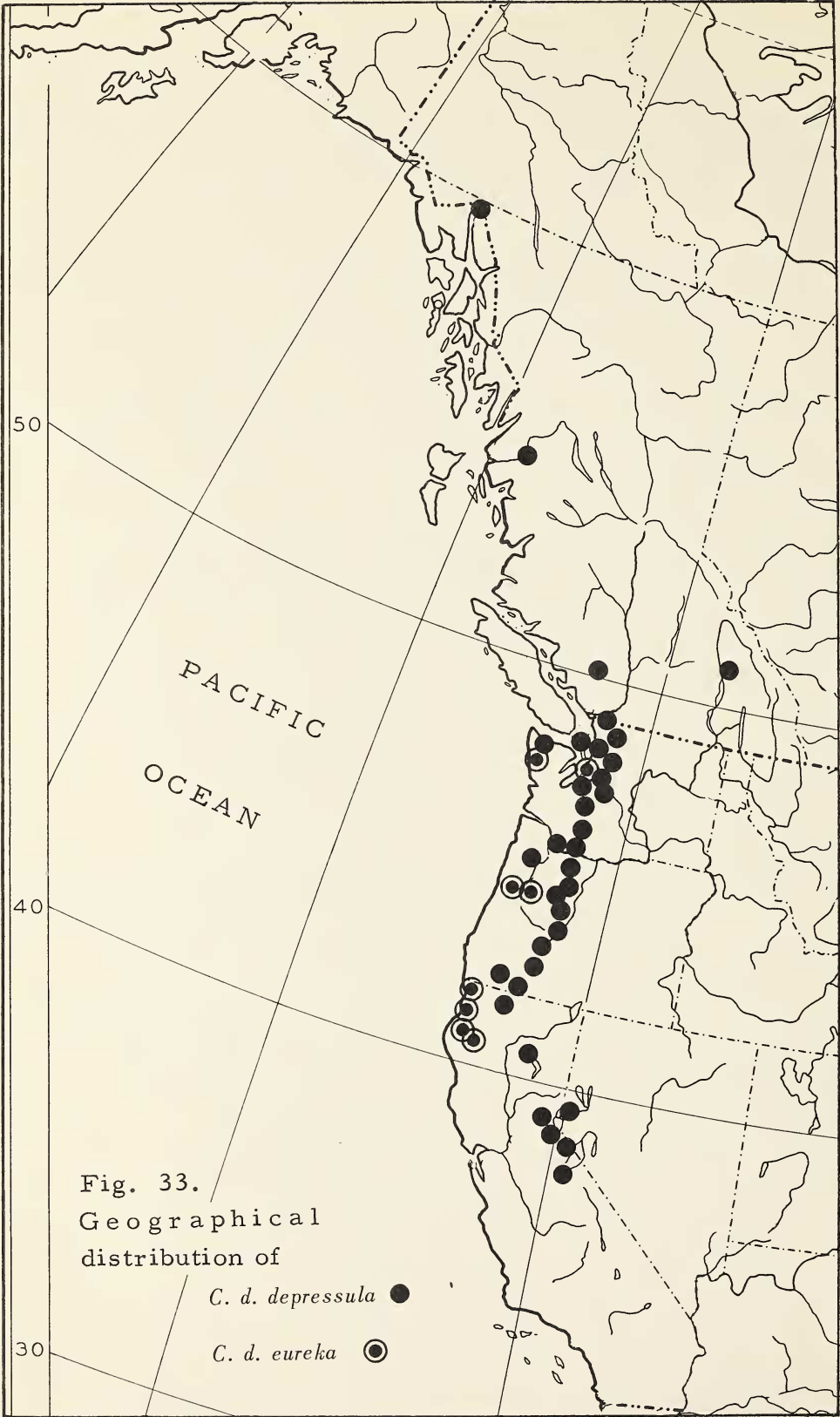
Mountain populations of California and Oregon are distributed in a thin band along the Cascade Range where they are confined to high altitudes, but further north they also occur in the Rockies (Mount Revelstoke, British Columbia) and altitudinal preference is not as marked as in southern regions (fig. 33).

TABLE 7 - Color variation of elytra and thoracic pleura of population samples of *Cicindela depressula*.

	Color of Elytra			Color of Pleural Sclerites		
	Brown	Green	Blue	Copper	Green	Blue
	N	N	N	N	N	N
d. depressula						
Haines, Alaska	1	4	0	4	1	0
Garibaldi Park, B. C.	1	7	7	8	6	1
Mount Baker, Wash.	1	5	6	2	6	4
Mount Rainier, Wash.	201	115	135	200	208	43
Mount Hood, Oregon	40	5	0	33	12	0
Crater Lake, Oregon	8	45	6	9	44	6
Lassen Nat. Pk., Calif.	0	22	1	1	21	1
Eldorado County, Calif.	0	25	1	1	24	1
d. eureka						
Orick, Red Ck., Calif.	12	0	0	3	5	4
Arcata, Mad River, Cal.	38	0	0	3	5	4
Van Duzen River, Calif.	41	5	0	5	31	10

TABLE 8 - The occurrence of elytral humeral dot and variation in the condition of the middle band of elytra among population samples of *Cicindela depressula*

	Specimens with dot/N	Specimens with complete band/N
d. depressula		
Haines, Alaska	5/5	4/5
Garibaldi Park, B. C.	14/15	13/15
Mount Baker, Wash.	11/12	12/12
Mount Rainier, Wash.	232/451	429/451
Mount Hood, Oregon	26/45	29/45
Crater Lake, Oregon	1/59	9/59
Lassen Park, Calif.	0/23	13/23
Eldorado County, Calif.	0/26	19/26
d. eureka		
Orick, Red. Creek, Calif.	12/12	12/12
Arcata, Mad River, Calif.	38/38	38/38
Van Duzen River, Calif.	46/46	46/46

50

PACIFIC

OCEAN

40

Fig. 33.
Geographical
distribution of

C. d. depressula ●

30   *C. d. eureka* ◉

Coastal specimens from California differ in external characteristics from alpine individuals at the same latitude. Specimens from these lowland regions usually have brown elytra, a very long, usually complete middle band, a humeral dot, and coppery, green, or blue thoracic pleura. They occupy river banks near the Pacific coast of northern California, Oregon and Washington. Few specimens of this type have been collected in Oregon and Washington. They may not be abundant in these regions; or perhaps the adults come out only for a short period. On the other hand, more intense collecting in May and June may yield larger numbers of these forms from these areas.

These differences provide the basis for distinguishing two subspecies: a southern coastal one, *d. eureka* Fall and a mountain northern one, *d. depressula* Casey.

Variation in some morphological characters, phenology, hybridization, and distribution of *depressula* and *eureka* have been discussed above. However, the apparently restricted distribution of *eureka* should be discussed further.

Distribution limits of *eureka* north of California are poorly understood because material is very scanty. In June 1963, a collecting expedition was made to the American southwest in order to obtain specimens of *depressula* and *oregona*. While in Humbolt County, California we obtained several large series of *eureka* near the mouths of Redwood Creek, and Mad and Van Duzen Rivers. Travelling from west to east in the Van Duzen River valley, we collected *eureka* as far east as Bridgeville which is approximately 1,000 feet above sea level and 30 miles east of the Pacific coast. Fifteen miles east of Bridgeville at an elevation of about 2,000 feet *eureka* was not present, nor was *eureka* present along Redwood Creek, 17 miles east of the Pacific coast. Thus the eastern limit of *eureka* is a short distance from the coast. At this latitude average temperature differences due to altitude may play a part in limiting *eureka* so closely to the coast. However, much ecological information is essential in order to understand the forces which confine *eureka* to such a restricted region in California.

C. depressula evolved in western North America probably as a cool-adapted lowland species, having shared a common ancestry with *duodecimguttata*. During a fairly recent glacial stage the range of the species was bisected by mountain glaciers with survivors to the west and to the east of the Cascades at low elevations. During this period of isolation differentiation occurred, with the coastal populations evolving the least in color pattern, but becoming bound to climatic conditions existing at lower elevations. This group became the subspecies *eureka*. As the glaciers retreated and the inland refugium became warmer and drier the populations isolated there (*d. depressula*) moved up the mountains or northwards or both ways. Differentiation then occurred in *d. depressula* with a loss of white markings in the southern members. In northern Washington the ranges of the two isolates met and hybridization took place.

Distribution patterns like that of *depressula* are evident in vertebrates such as *Sorex vagrans* Baird (Findley 1955), *Rana aurora*, Baird and Girard, and *Contia tenuis* Baird and Girard (Stebbins 1954).

Distribution

Of the 922 specimens of *depressula* examined, one appears to be incorrectly labelled Berkeley, Alameda County, California. This specimen does not resemble the subspecies *d. eureka* but it is phenotypically *d. depressula* the distribution of which is restricted to the Cascade Range at that latitude.

Cicindela depressula depressula Casey. Canada. BRITISH COLUMBIA: Diamond Head Trail, Garibaldi Park, 14; Jade Lake Trail, Mount Revelstoke, 1; Terrace, 4. United States. ALASKA: Haines Highway, near Haines, 5. CALIFORNIA: Alpine County: 7. Eldorado County: Echo Lake 15; Fallen Leaf Lake, 2; Keith Dome, 11; Mount Tallac, 10; Summit, 3. Mariposa County: Kerrick Meadows, Yosemite National Park, 2. Nevada County: Rucker Lake, 1. Placer County: Summit, 2. Shasta County: Kings Creek, Lassen Park, 6; Mount Lassen, 18. Siskiyou County: Walker, 3. Localities of unknown counties: Angora Park, 3; Carson Pass, 2; Charity Valley, 1; Sovoft, Sierra Nevada Mountains, 1; Warner Valley, 2. NEVADA: Washoe County: Mount Rose, 2. OREGON: Deschutes County: Three Creeks, 1; Todd Lake Meadows, 1. Douglas County: Diamond Lake, 1; Three Lakes, 1. Hood River County: Mount Hood, 54. Jackson County: Mount Ashland, 2. Jefferson County: Mount Jefferson, 1. Josephine County: Rogue Riffles, 1. Klamath County: Crater Lake, 60; Summit Lake, 2. Lake County: Linton Meadows, near Three Sisters area, 17. Lane County: Obsidian Trail, 1; Scott Lake, 9; Wikiup Plains, 5. Linn County: Big Lake, 1; Hoodoo, 2; Santiam, 1. Yamhill County: McMannville, 1. WASHINGTON: Clallam County: Forks, 6. Clark County: Vancouver, 4. Cowlitz County: Silverlake, 2. King County: Enumclaw, 1; Red Mountain, 1. Kittitas County: Cle Elum, 1. Pierce County: 1; Long Mire, 3; Mount Rainier, 461. San Juan Islands, 1. Skamania County: Little Huckleberry Mountain, 1. Snohomish County: Arlington, 3; Soda Springs, 1; Sultan, 1. Whatcom County: Mount Baker, 9. Yakima County: Naches Pass, 4. Localities of unknown counties: Chinook Pass, 8; Greenwater, 2; Lake Cushman, 3; Mora, 2; Mount Adams, 13; Pilchuck Mountain, 1; Stillguamish, 2; Verlot, 1.

Cicindela depressula eureka Fall. United States. CALIFORNIA: Humbolt County: Alton, 2; Arcata, Mad River, 39; Blue Lake, 4; Bridgeville near Van Duzen River, 19; Fortuna, 1; Orick, Redwood Creek, 12; Scotia, 1; Van Duzen River, 27. Del Norte County: Requa, 3; Terwah, 1. OREGON: Benton County: Corvallis, 1. Linn County: Albany, 1. WASHINGTON: King County: Seattle, 1. Whatcom County: Naches Pass, 1.

HYBRIDIZATION BETWEEN *C. OREGONA* AND
C. DUODECIMGUTTATA

Introduction

Cicindela duodecimguttata ranges across most of eastern and central North America from Texas to northern Canada, and from the eastern slopes of the Rocky Mountains to the Atlantic (fig. 17). *Cicindela oregona* occupies regions in and west of the Rocky Mountains to the Pacific coast from southern United States to Alaska (fig. 18).

During the glacial stages of the Pleistocene the two forms were probably isolated from one another, *oregona* to the west of the Rockies and *duodecimguttata* to the east of that mountain range. Since Pleistocene times their ranges have expanded and have come together forming a zone of intergradation on the eastern slopes of the Rocky Mountains, that extends from Colorado to northwestern Canada. This hybrid zone is approximately 50 miles wide in the North Saskatchewan River valley in western Alberta, but it is nearly 1,000 miles wide in northwestern Canada. As far as is known hybridization between these two species occurs in all areas of sympatry.

This study is based on 19 population samples comprising 1,731 adult specimens of which 1,291 were collected in Alberta, 205 in the Northwest Territories, 75 in British Columbia, 70 in Montana, 61 in Saskatchewan, 27 in Alaska and 3 in Colorado (see fig. 34). Additional material from areas east and west of the hybrid zone was obtained from various North American institutions and has been analyzed in the *oregona* and *duodecimguttata* taxonomic sections.

Adult male and female *duodecimguttata* are alike in color, color pattern, and distribution of hair on the head. Hairs cover the frons, top of the
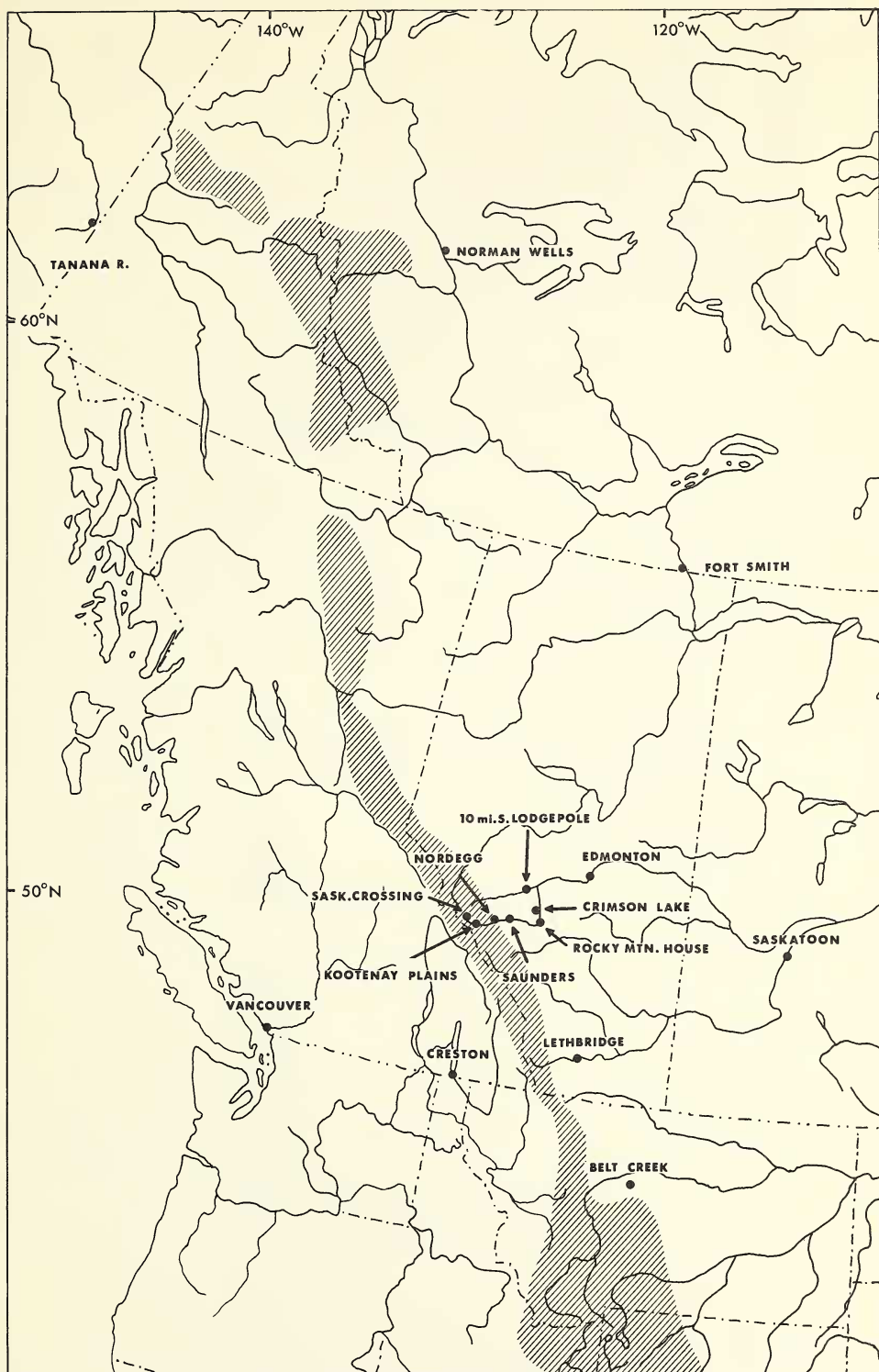
Fig. 34. Locality map of population samples analyzed by hybrid index method. Dark areas indicate elevations above 5,000 feet.

head and post genae. In the western portions of the range of this species individuals are brown dorsally and metallic blue-green ventrally, the prothoracic pleura are coppery, and they have complete elytral patterns (for details see p. 102).

     The species *duodecimguttata* hybridizes with the subspecies *oregona guttifera.* Both sexes of this subspecies have similar external features. Hairs are not present on the post genae, frons or top of the head, but a few occupy a small area near the front inner edges of the eyes. The color is identical to that of *duodecimguttata* - brown dorsally and blue-green ventrally, and coppery prothoracic pleura. A reduced elytral pattern is character- istic of *oregona* with humeral and apical lunules each represented by two dots, and the marginal band absent.

     Elytral pattern, and distribution of hair on the head were used to develop a hybrid index for *duodecimguttata* and *oregona*. Male genitalia were not used because it seemed preferable to use characteristics occurring in both sexes. High values were assigned to the characteristics of *duodecimguttata*, low to those of *oregona*. Intermediate expressions of these char- acteristics were scored with intermediate values. These characteristics are illustrated in figs. 11 to 16 and details of assignment of values are given in table 9. In population samples of non-hybrid *duodecimguttata* f r o m western localities, index values range from 4 to 7; and in non-hybrid popula- tions of *oregona*, values range from 0 to 1.

TABLE 9 - Values assigned to diagnostic characters of *C. duodecimguttata* and *C. oregona* used in determination of compound character indices.

Elytral markings and areas of head	Values		
	0	1	2
Humeral lunule	two dots	broken	complete
Marginal band	absent	broken or trace	complete
Apical lunule	two dots	complete	-
Frons	glabrous	hairy	-
Post gena	glabrous	hairy	-

     Characteristics of *oregona* and *duodecimguttata* occur in many recomb- inations in the hybrids. Many specimens are like one of the parental types except for one character while others have index values of 2 or 3. Specimens that have hairs on the frons and head often have hairy post genae. This could be a pleiotropic effect of a single gene, but since the association is inconstant the post genae and frons are treated as separate characters.

Variation in Space

     A hybrid index value was determined for each of the 1,731 spec- imens. A histogram shows the percentage of specimens per index value for each population sample (figs 35-44). The localities from which population samples were collected are illustrated in fig. 34 except those that are represented by only a few specimens.
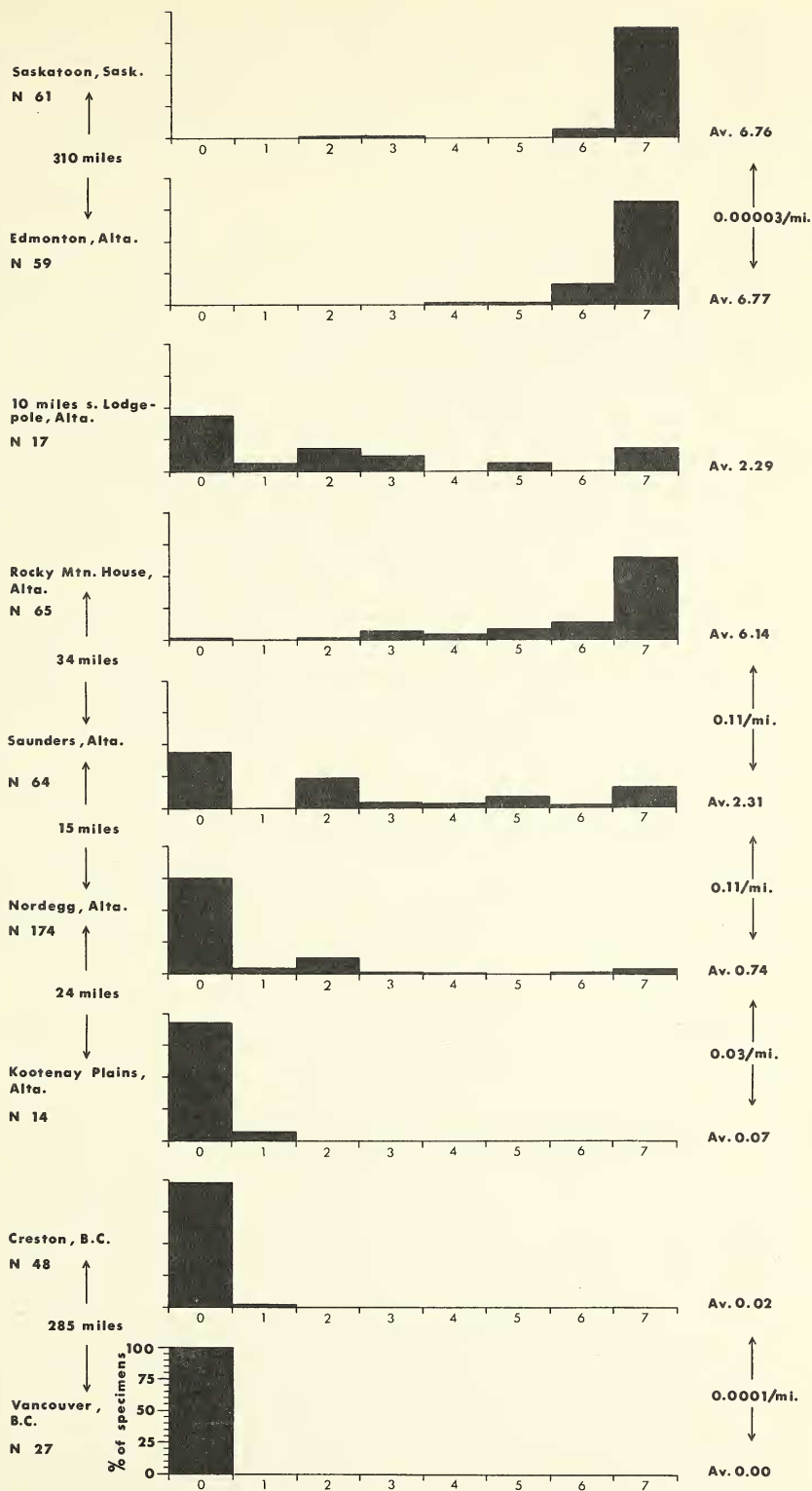
Fig. 35. Changes in the frequency distribution of hybrid index values in population samples of *C. duodecimguttata* and *C. oregona* between Saskatoon and Vancouver. Average hybrid indices and the change in hybrid index per mile on the right, number of specimens and air miles between localities on the left.

cussion; a transect from Vancouver, British Columbia to Saskatoon, Saskatchewan, via the Saskatchewan River System; the Belt Creek, Montana sample; the Boulder, Colorado sample; and a transect from Tanana River, Alaska to Fort Smith, Northwest Territories through Norman Wells, Northwest Territories.

Vancouver –Saskatchewan River Drainage Transect

In figure 35 three portions of the transect serve to illustrate spatial phenotypic changes between uncontaminated populations of *oregona* and uncontaminated *duodecimguttata* through a zone of intergradation centered in the upper regions of the North Saskatchewan River valley. The transect lies on a west-east plane with the geographically extreme points Vancouver in the west and Saskatoon in the east. The first part includes population samples from Vancouver and Creston. The second portion of the transect is along the western regions of the North Saskatchewan River valley and includes population samples from Kootenay Plains, Nordegg, Saunders, Rocky Mountain House, and Lodgepole. The Edmonton and Saskatoon samples constitute the eastern portion of the transect. Air mile distances and index changes per mile between localities are also given in the figure. Histograms illustrating variation in population samples from Lethbridge, Saskatchewan Crossing, Garth, Crimson Lake, and eight miles south of Lodgepole provide additional data.

Specimens collected in Vancouver, British Columbia on a sand bank bordering an inlet of the Pacific Ocean all score 0 indicating a pure *oregona* population.

The sample collected at Creston, 285 air miles east of Vancouver, is composed of 48 specimens of which 21 were taken by Stace-Smith in 1945 and 27 by Ball in 1957. Only one specimen scores 1, while the remaining score 0. Average index change per mile, from Vancouver to Creston is 0.0001 which is negligible and can be attributed to natural variation in the Creston population.

In 1962 specimens were collected near the Kootenay Plains, 20 miles down stream from the junction of the Banff-Jasper highway and the North Saskatchewan River. River banks are steep near the Plains and are covered with undergrowth to the edge. These banks are therefore not suitable for riparian tiger beetles such as *oregona* . However, many islands formed by sand and clay deposits occupy the river bed and divide the river into several large streams. Most of these islands are sparsely covered with grass and shrubs, and river debris such as drift wood is plentiful. The islands proved to be suitable habitat for *oregona* and another riparian species, *C. repanda.* One specimen scores 1, the other 13 all score 0. The average index value for the sample is 0.07.

Sand and mud islands that characterize the North Saskatchewan River near Kootenay Plains are also present 24 miles down stream at the Forestry Trunk Road crossing near Nordegg. Two islands divide the river into three large streams. Three road bridges link the islands with one another and the river banks. The southern island bears large shrubs which occupy higher central portions, while grass is abundant throughout. Much of the west half of the island is a clay flat that is periodically covered with water when the river rises. The soil there is basic with a pH of 8.2. There is little organic matter in the soil but

much free lime. Riparian tiger beetles are abundant on the island esp-
ecially along the clay flat. A series of 174 specimens was collected in
1963;the population sample is variable, composed of *oregona, duodecimguttata,*
and hybrid individuals. The index values range from 0 to 7, with the
average at 0.74.   Of the population sample 76 per cent score 0,
four per cent score 7, and 26 per cent have intermediate values. The
average index value increases 0.03 units per air mile from Kootenay
Plains to Nordegg, which is 300 times greater than that from Vancouver
to Creston.

Fifteen air miles east of Nordegg near Saunders the North
Saskatchewan River is narrow and there are no islands. The north shore
is a sandy strip several to 10 feet wide and littered with drift wood.
The river banks descend sharply to the sandy shore line, and are covered
with undergrowth for the most part but grassy clearings are present.
These clearings are probably periodically inhabited by riparian tiger
beetles when the river is high and covers the sandy shore margins.
C. oregona , *duodecimguttata* and hybrid individuals are abundant on the beach
at Saunders from which a series consisting of 64 specimens was taken
in 1963.

The range in index values is 0 to 7 with the average at 2.31. This
is a mean index increase of 0.11 per mile from Nordegg to Saunders,
that is, more than three times the average index increase per mile from
Kootenay Plains to Nordegg. Specimens with an index of 0 comprise
43.8 per cent of the population sample, while those which score 7 con-
stitute 15.6 per cent. Individuals which score 2 to 6 inclusive make up
40.6 per cent of the sample. No specimen has an index value of 1.

Thirty-four miles east of Saunders, at the Highway 11 bridge
near Rocky Mountain House, the river banks are flatter and broader
than those upstream. A mixture of clay, sand and loose gravel forms
the south bank near the bridge. Open patches on which tiger beetles are
active are common.

The index values range from 0 to 7 and the average is 6.14.
Specimens scoring 7 comprise 64.7 per cent of the population sample
while individuals with a value of 0 constitute 1.5 per cent. Most
hybrids resemble *duodecimguttata* more closely than *oregona*. Although non-
hybrid *oregona* is scarce in this predominantly *duodecimguttata* population
many hybrid individuals are present.

Ten miles south of Lodgepole large sand banks flank the north
side of the Brazeau River adjacent to the Brazeau power house. Because
a dam has been erected further upstream, only a little water is present
near the power house and much of the river bed is exposed. On August
12, 1963 a population sample was collected on the sand banks near the
Brazeau power house.

The specimens have index values that range from 0 to 7 but none
score 4 or 6. The average index is 2.29. Because the Brazeau power
house is located near the North Saskatchewan River between Rocky Mount-
ain House and Edmonton, it would appear that the mean index value of a
population sample from that area should fall between 6.14 and 6.77, the
average indices of Rocky Mountain House and Edmonton respectively.

In fact, the average index is approximately 4 less than expected. This may be in part because the Brazeau power house locality although downstream from Rocky Mountain House is 17 miles west of it. In addition, *oregona* and *duodecimguttata* exhibit different habitat preferences (see locality eight miles south of Lodgepole). The pure sand bank near the power house is particularly suitable for *oregona* and harbors a population with a lower average index value than that at Rocky Mountain House.

A sample was collected in 1961 near the Groat Bridge in Edmonton. The average index value is 6.77 and the range is 4 to 7 inclusive. This may be the result of hybridization with *oregona* but is more likely natural variation.

The mean index value of the Saskatoon sample is 6.76 which is a change of 0.00003 index units per mile from Edmonton to Saskatoon a distance of 310 air miles. A small percentage of the sample with values of 2 and 3 is interpreted as natural variation in a non-hybrid *duodecimguttata* population. It is the result of breakdown of the elytral markings, which is probably caused by *duodecimguttata* genes infiltrating from the east, rather than *oregona* genes from the west.

Additional localities in western Alberta

Ten specimens were collected near the junction of the North Saskatchewan River and Banff-Jasper Highway about 20 miles west of the Kootenay Plains. All the individuals score 0 (fig. 36).

Garth is approximately three miles upstream from Rocky Mountain House. The river on the north side is a clear stretch of sand and clay. In May, 1963 a sample was taken on this beach. The index values range from 0 to 7. Most specimens score high and the average index is 5.25 (fig. 37). If this is compared with the histogram for the Rocky Mountain House sample (fig. 38), that was collected on the same day, the mean index difference is 1.24.

Crimson Lake is about nine miles north of Rocky Mountain House. At the east end the water front is sandy. For about 500 feet and at the south end of this beach the sand is light in color and loose and *C. repanda* is abundant. Toward the west end of the beach the ground is a hard and dark mixture of sand and clay and is flanked by a marshy area. Many *duodecimguttata* individuals were active in this area of the beach and *repanda* was absent. Samples were collected at Crimson Lake in 1961, 1962, and 1963. The range of average index values is 6.14 to 6.55 (fig. 39). Several *oregona* specimens were collected here but they are rare. The population is mainly *duodecimguttata* with evidence of *oregona* gene infiltration.

Between Lodgepole and the Brazeau power house many ponds are scattered beside the gravel highway. These are water-filled gravel pits that were dug out for road construction. The soil around the ponds is normally hardened clay covered with grass. The same day the Brazeau power house specimens were taken, I also collected 17 specimens near one of these roadside ponds eight miles south of Lodgepole. The hybrid index values of the roadside samples range from 3 to 7, and the average index is 6.36 (fig. 40). This index average is 4.07 more than the mean index of the Brazeau power house population.

The marked average index difference between populations of the
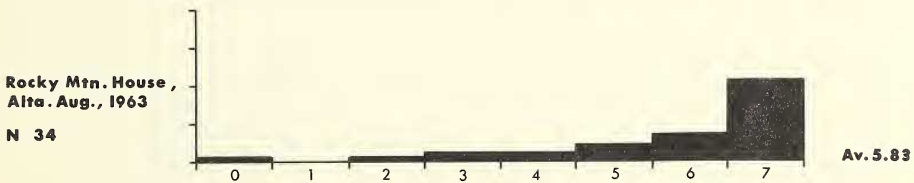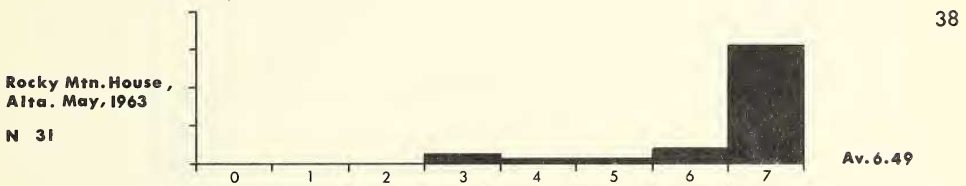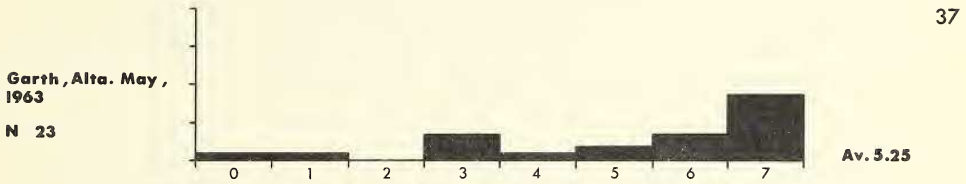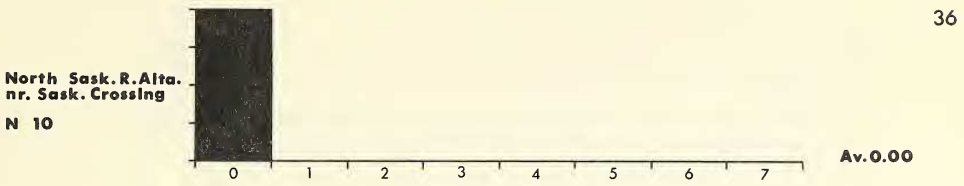
Figs 36-38. Frequency distribution of hybrid index values in population samples of, 36, *C. oregona* from Saskatchewan Crossing, Alberta; 37, *C. oregona* X *C. duodecimguttata* from Crimson Lake, Alberta. N. = no. of specimens.

Brazeau power house and roadside ponds is indicative of different habitat preferences of the two species. Populations of *oregona* are best adapted to pure sand and clean gravel. commonly found along mountain streams. The species *duodecimguttata* normally inhabits edges of lakes, sloughs, and rivers where there are usually flat clearings of dark sand, clay or mud. Wherever these two habitats are available together, at least near the North Saskatchewan River, *duodecimguttata* and *oregona* hybridize. Because the soils around the roadside ponds between Lodgepole and Brazeau power house are predominantly clay, they were probably first inhabited by *duodecimguttata* which invaded these ponds from sloughs etc. nearby. However the effect of *oregona* is evident in these roadside populations.
        The Lethbridge sample consists of 310 specimens that were
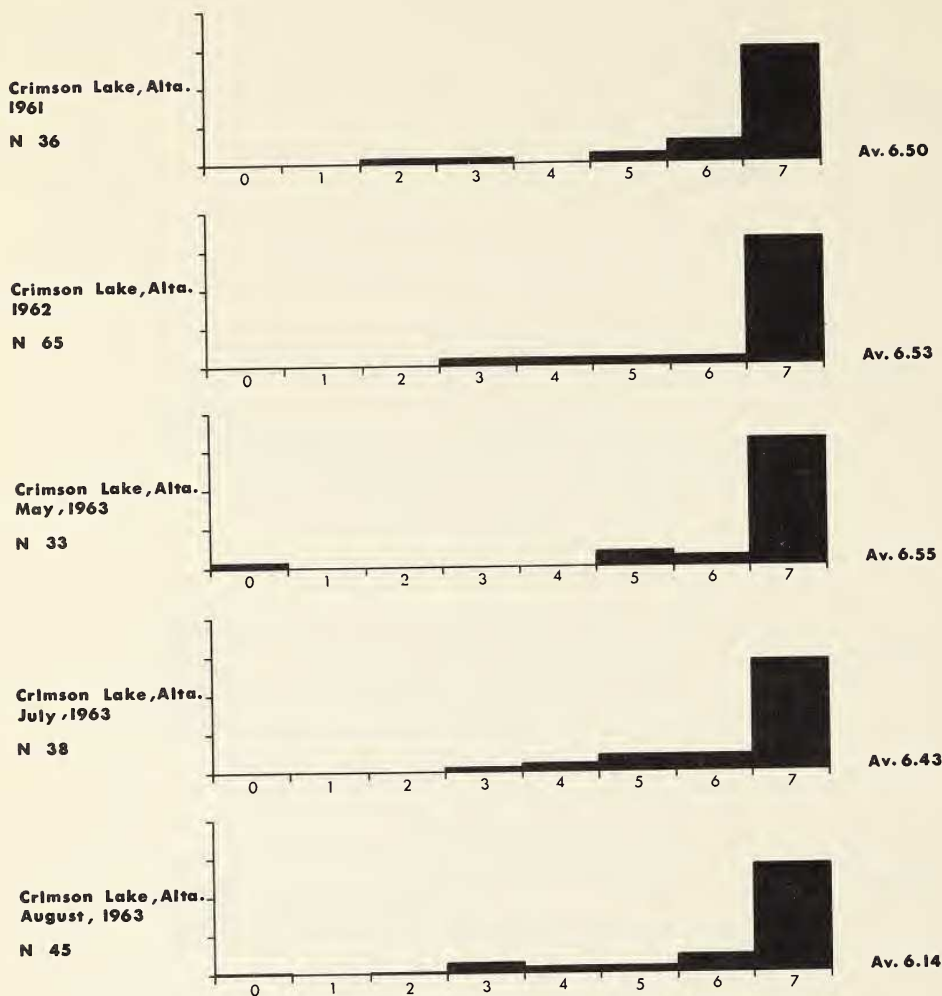
Fig. 39. Frequency distribution of hybrid index values in five population samples of *C. oregona* X *C. duodecimguttata* from Crimson Lake, Alberta. N. = no. of specimens.

collected throughout the summer of 1962 (fig. 41). More than 84 per cent of the specimens are pure *duodecimguttata*. No individuals score 0 or 1. The index range is 2 to 7 inclusive with the average at 6.7. The histogram indicates that some introgression from *oregona* is influencing this predominantly *duodecimguttata* populati on. In 1960 two *oregona* specimens were collected near Lethbridge. The occurrence of these specimens supports the supposition that variation in Lethbridge is the result of hybridization between *oregona* and *duodecimguttata*.

High River is 30 miles south of Calgary. Of the four representative specimens there are two hybrids, one *oregona* , and one *duodecimguttata*.

In 1925 F. S. Carr collected eleven specimens from H a p p y

8 miles s. Lodge-pole, Alta. July, 1963

N 19

40

Av. 6.06

8 miles s. Lodge-pole, Alta. August, 1963

N 17

Av. 6.36

Lethbridge, Alta. 1962

N 310

41

Av. 6.66

Belt Ck. e. Armington, Mont. 1963

N 70

42

Av. 1.23
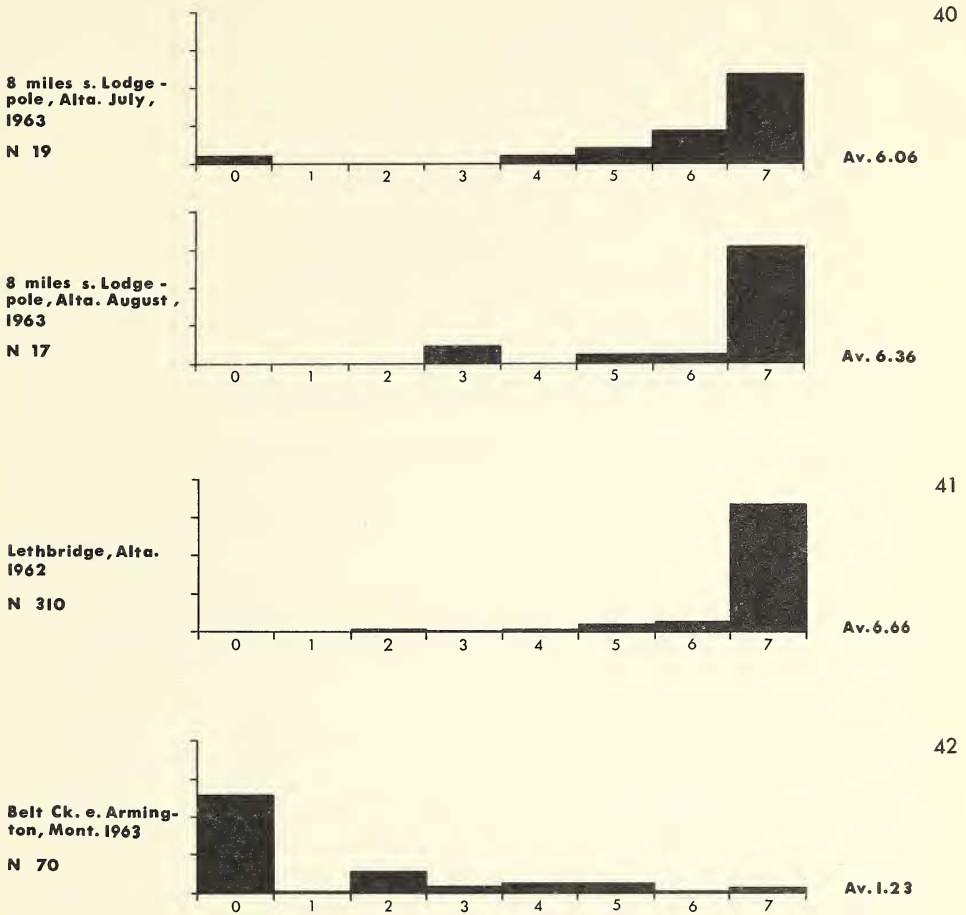
Figs 40-42. Frequency distribution of hybrid index values in population samples of, 40, *C. oregona* X *C. duodecimguttata* from 8 mi. south of Lodgepole, Alberta (2 samples); 41, *C. oregona* X *C. duodecimguttata* from Lethbridge, Alberta; 42, X *C. duodecimguttata* from Belt Creek near Armington, Montana. N. = no. of specimens.

Valley which is near the Bow River approximately four miles west of Calgary. The sample consists of six *oregona*, two *duodecimguttata* and three hybrids.

Three specimens were taken in 1961 by Wu near Ricinus along the Clearwater River, 20 miles south of Rocky Mountain House. Two individuals are *duodecimguttata* and one is a hybrid.

Two specimens of *duodecimguttata* and one hybrid were collected at Beaver Creek, Alberta. The locality and collector of this small sample are both unknown.

Belt Creek, Montana

In 1963 a sample was collected along Belt Creek just east of

Arlington, Montana.   Specimens of both *oregona* and *duodecimguttata* were taken with hybrids. All of the index values are represented, but *oregona* specimens represent 64.3 per cent of the sample while two indiv- iduals score 7 and constitute 2.9 per cent of the series. The index mean is 1.23 (fig. 42).

There are mean differences in index values between males and females.   Values for males do not exceed 5, and the mean index value is 0.70.   Thirty-four females show a range in values from 0 to 7 and their average index is 1.79;that is, 1.09 more than the males which total 36. In other samples, the differences between males and females is less.

Boulder, Colorado

The southernmost hybrid sample is represented b y two *duodecimguttata* specimens and one hybrid which were collected four miles north of Boulder,   Colorado in July 1960. A histogram is not provided for this sample.

The Alaska - Fort Smith Transect

This transect, composed of population samples collected at the Tanana River, Alaska, Norman Wells, Northwest Territories, and Fort Smith, Northwest Territories extends over a range of about 1,000 miles (fig. 34). Index values were determined for all of the specimens and a histogram is presented for each of the three samples (fig. 43). Included in the figure are air mile distances and index changes per mile between the localities.

In 1958 Ball collected a series of specimens at a junction of the Tanana River and the Alaska Highway in southeastern Alaska. Specimens that have an index value of 0 constitute 88.9 per cent of the sample, while two individuals, representing 11.1 per cent each score 1, because both have hairs on their heads. The average index value is 0.11.

Norman Wells, situated near the Mackenzie River, is approxi- mately 470 miles east - northeast of the Tanana River locality. Index values range from 0 to 7 with the average at 2.68. The average index change per mile from Tanana River to Norman Wells is 0.00547. The sample exhibits a great amount of variation and hybrids outnumber the parental forms. One specimen scores 0 and two members each have values of 7.   Thus the parental specimens together constitute only 6.9 per cent of the sample. In contrast individuals that score 2 occur in the greatest frequency and make up 69.9 per cent of the sample. It has been pointed out earlier that natural variation in an uncontaminated *duodecimguttata* sample may include specimens indexed from 2 to 7. Similarly a pure *oregona* population can have individuals that score 1 as well as 0. Thus a true hybrid is considered to have a value of 2 or 3. Because speci- mens with scores of 2 and 3 dominate the Norman Wells sample it is regarded as a predominantly hybrid population sample and is the only one of its kind in this study.

A sample was collected at Fort Smith near the Slave River, 580 miles southeast of Norman Wells. Index values range from 2 to 7 with the average at 5.97. From Norman Wells to Fort Smith the change per mile is 0.00567 units. No specimens have values of 0 or 1. Individuals that score 2 occur in lowest frequency while those with a value of 7 are

43

Tanana R., Mi.1281
Alas. Hway. Alas.

N 27

470 miles

Norman Wells,
N.W.T.

N 43

580 miles

Fort Smith, N.W.T.

N 162
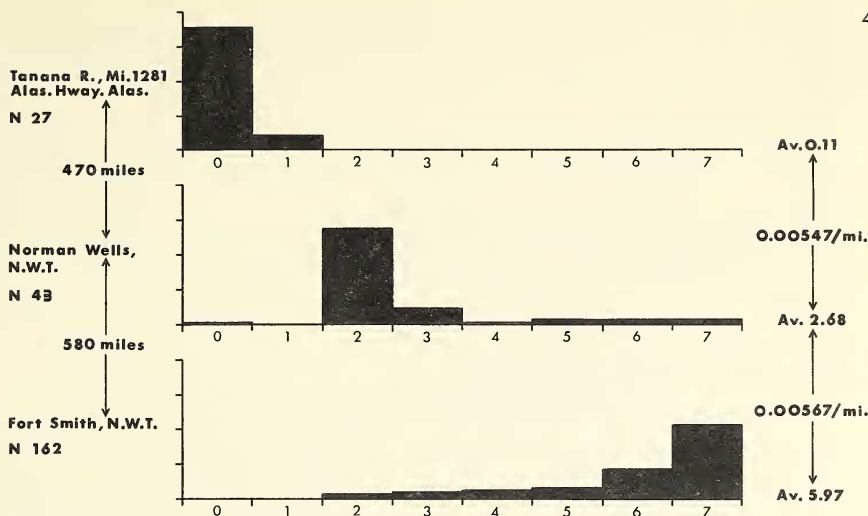
Av. 0.11

0.00547/mi.

Av. 2.68

0.00567/mi.

Av. 5.97

Fig. 43. Frequency distribution of hybrid index values in population samples of *C. oregona* X *C. duodecimguttata* from Alaska and the Northwest Territories. Average hybrid indices and the change in hybrid index per mile on the right, number of specimens and air miles between localities on the left.
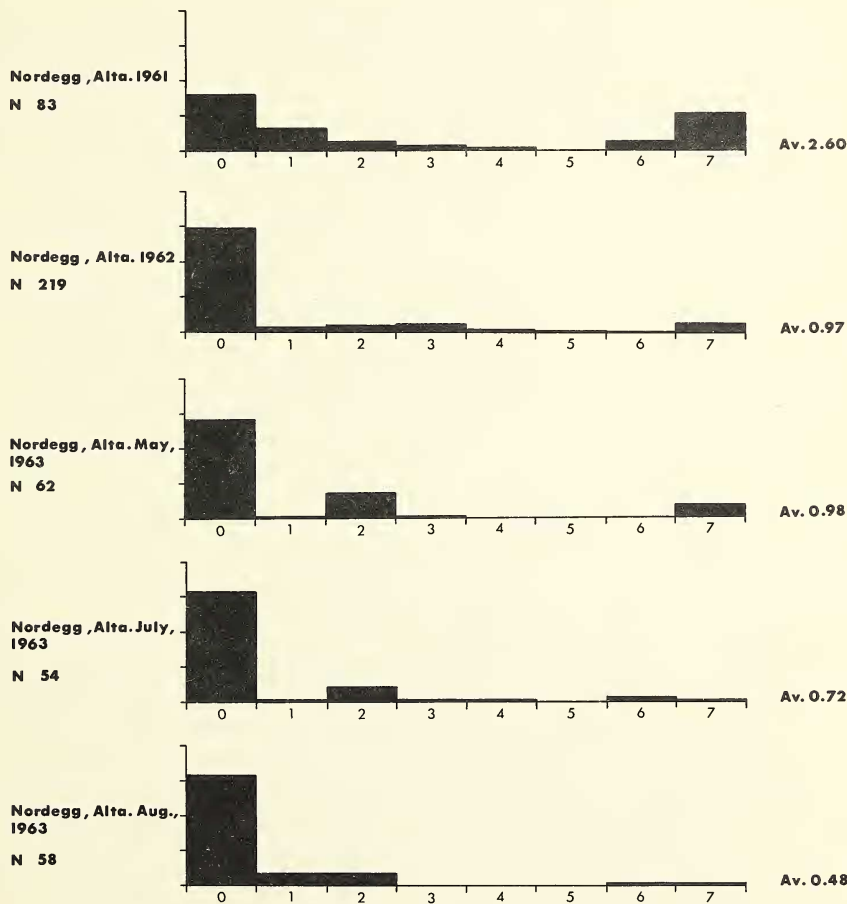
44

Nordegg , Alta. 1961

N 83

Av. 2.60

Nordegg , Alta. 1962

N 219

Av. 0.97

Nordegg, Alta. May,
1963

N 62

Av. 0.98

Nordegg ,Alta. July,
1963

N 54

Av. 0.72

Nordegg, Alta. Aug.,
1963

N 58

Av. 0.48

Fig. 44. Frequency distribution of hybrid index values in population samples of *C. oregona* X *C. duodecimguttata* from Nordegg, Alberta. N. = no. of specimens.

most numerous.   The number of specimens increases with increasing index values.   The sample is therefore a *duodecimguttata* one affected by introgression of *oregona* characteristics.

Of the five specimens taken at Canol near the Mackenzie River opposite Norman Wells there are one *oregona,* one *duodecimguttata* and three hybrids.

One *oregona* specimen and one hybrid were taken at Fort Simpson which is 290 miles southeast of Norman Wells near the mouth of the Liard River.

Variation in Time

Annual and seasonal variation in index values appear to be typical of most localities in the western section of the North Saskatchewan River. Variation is illustrated by histograms for population samples collected in the Nordegg area, near Rocky Mountain House, at Crimson Lake, and in an area eight miles south of Lodgepole.

Nordegg

Evidence of extensive hybridization is clearly shown in the histogram for the 1961 sample (fig. 44). Index values range from 0 to 7 and the average is 2.60. Specimens of *oregona* are most common, constituting 39.8 per cent of the sample. Specimens of *duodecimguttata* follow in number and are 25.3 per cent of the sample. The remaining portion of the series is formed by intermediate specimens which are mainly at the low end of the index scale.

The situation is markedly changed in 1962. A shift toward the low end of the histogram occurs. Specimens that score 0 increase to 74.2 per cent, while specimens with an index of 7 drop to 6.8 per cent of the sample. The average index is 0.97, a drop of 1.63 from the previous year. There is a further depletion in *duodecimguttata* numbers in 1963 but there is very little general change in the frequency of indices from that of 1962.

This may be a phase in fluctuating populations of the parental forms. However many more years of sampling at Nordegg would provide a clearer picture of annual variation in these populations. Analysis of Nordegg population samples collected in May, July, and August, 1963, revealed a slight trend in decrease of average index values throughout the summer.

Values for the May sample, range from 0 to 7, excepting 4, 5, and 6, with the average at 0.98. The sample is therefore predominantly *oregona* specimens (71 per cent), some hybrids closely resembling *oregona,* and five phenotypic *duodecimguttata* individuals.   In the July sample more classes are present, and only index value 5 is not represented.   The index value is 0.72, which is 0.26 less than that of May. Specimens with high index values are all but absent from the August sample. Most of the specimens are at the low end of the scale with the largest number at 0.

There also appears to be a seasonal change in the relative numbers of males and females at Nordegg. The ratio of males to females in the May population sample is approximately 3 to 4 (27 males and 35 females), but males outnumber females in the July sample, 2 to 1 (36 males and

18 females).   In the August series, the ratio of males to females is approximately 3.5 to 1 (45 males to 13 females).

Rocky Mountain House

The range in index values for the May series is 3 to 7 with the average at 6.49. Of the sample, 24 specimens score 7. Thus the population sample is basically a *duocecimguttata* one somewhat contaminated by *oregona* genes (fig. 38). The August sample is more variable and all the index values except 2, are represented. The average index value is 5.83 which is a decrease of 0.66 from the May value.

Relative members of males and females also change seasonally, and parallel the change which occurs at Nordegg. The ratio of males and females in May is 1 to 1 (15 males and 16 females), while in August there are approximately three times as many males as females (26 males and 8 females).   This difference however is not statistically significant.

Crimson Lake

The histogram for specimens collected at Crimson Lake in 1961 shows a mainly *duodecimguttata* population (fig. 39). One specimen has an index value of 2 and one has a value of 3. The mean index is 6.50. The range of index values for 1962 is 3 to 7 with the mean value at 6.53. The average index change from 1961 to 1962 - 0.03 - is quite small. In 1963 the mean value decreased by 0.19, and the range in index values is 0 to 7.   The population sample however is largely a *duodecimguttata* one much like those of the two previous years. The major difference is that *oregona* specimens are present in the 1963 series, but they are rare.

From May to August a general decrease occurred in the mean index values of the Crimson Lake samples. This seasonal index change corresponds with that of Nordegg and Rocky Mountain House.

Ten males and 23 females in May, 21 males and 17 females in July, and 25 males and 20 females in August were collected in 1963. The sex ratio is two females to one male in the May sample, but is one to one for July and August.

Lodgepole - eight miles south

In 1963, small series of 19 and 17 specimens were collected at this locality in July and August respectively. Seasonal differences between the two samples do not coincide with those of Nordegg, Crimson Lake, and Rocky Mountain House but the samples are probably too small to indicate real differences.   However there seems to be a shift from a lower average index value earlier in the season to a higher average value later in the season.   Both samples consist mainly of *duodecimguttata* specimens but with a few hybrids (fig. 40).

The males and females are present in about equal numbers in both population samples, with nine females and 10 males taken in July, and nine females and eight males collected in August.

Notes on mating

During the summer of 1962, in the Nordegg area, 26 pairs of mating tiger beetles were collected. This is a phenotypically varied

group, including both parental species and hybrids. Hybrid indices were determined for the specimens. Then, a chi square test for independence was applied to find out if specimens of a particular index more often selected a mate of the same index value. It failed to show any selection in mating.

On several occasions I have taken *repanda* in copulation with *oregona* and also with *duodecimguttata*, but no hybrids have been found. It is doubtful that gene exchange takes place between *repanda* and *oregona* or *duodecimguttata*, to the extent that it does between *oregona* and *duodecimguttata*.

Discussion

The kind of hybridization between *oregona* and *duodecimguttata* can be classified as one of introgression (Anderson 1949), and secondary intergradation (Mayr 1942). Introgression, as described by Anderson, is the incorporation of genes of one species into the gene complex of another species. Mayr states that secondary intergradation has occurred when "Two units, now connected by a steeply sloping character gradient were separated completely at one time and have now come into contact again after a number of differences have evolved." Mayr (1963) regards the species involved in this kind of hybridization as semispecies in that they show some of the characteristics of a species and some of subspecies. Many such cases have been described for birds, mammals, fish, amphibians and some invertebrates. These are too numerous to mention here but many are cited by Dobzhansky (1951), Mayr (1942, 1963), Mecham (1961), and Sibley (1961).

The situation in western Alberta and northwestern Canada described above seems to be the result of secondary contact between the formerly isolated vicariant species *oregona* and *duodecimguttata*. Their phenotypic differences probably arose under different selective forces acting on allopatric populations. Breakdown of external barriers between them allowed their ranges to expand and come into contact. This has resulted in hybridization. Speciation of *oregona* and *duodecimguttata* was probably initiated in early Pleistocene times, but the process has not been completed. Climatic changes during the Pleistocene undoubtedly had a profound influence on the distribution of these two forms as they did on other North American animal species (see Blair 1951). Unlike the vertebrates, however, neither locations of refugia for these tiger beetles nor their population movements during the Pleistocene are known because of the lack of a fossil record. The history of this zone of secondary intergradation is therefore speculative, and is based on the present distribution of both species, and current concepts of events during the Pleistocene. During the early period of *oregona* subspeciation, populations of *duodecimguttata* were not present in western regions they now occupy. Shortly after the development of *o. guttifera*, perhaps *duodecimguttata* reinvaded western Canada east of the Rocky Mountains. Because, at the present time, few southern populations of *duodecimguttata* reach the eastern front of the Rockies in Colorado and New Mexico, the present western limits are presumed to be the extent of the western limits of *duodecimguttata* during the late Prairie interglacial. If any hybridization did occur in Prairie times it took place where the two species are presently sympatric. However, any evidence of pre-Recent introgression would be masked by the present hybrid belt. Hybridization probably did occur in southern

regions during the Wisconsin glaciation since no indication of introgression is evident in southern populations.

The hybrid belt between *oregona* and *duodecimguttata* is widest in northwestern Canada and narrowest in western Alberta. Individual specimens of *oregona* and *duodecimguttata* exist in all areas of greatest variability including the Norman Wells population where they are outnumbered by intermediates. Width of the zone of intergradation is recognized as spatial limits of extreme variation.

There does not seem to be any reduced viability or fertility in the hybrid tiger beetles and they are present in large numbers in the Norman Wells sample described above. A composite of isolating mechanisms, although hardly pronounced in southern populations of *oregona* and *duodecimguttata*, may have become more completely developed than in northern populations of the two species before they made contact. This may account in part for the varying width of the zone of intergradation between *oregona* and *duodecimguttata*.

Somewhat analogous is the intergradation zone of the European crows *Corvus corone cornix* and *C. c. corone* (Mayr 1942, pp. 265-266), and that of the North American grackles *Quiscalus quiscula quiscula* and *Q. q. versicolor* (Huntington 1952). Dobzhansky (1951) attempts to explain the irregular width of the intergradation belt of the crows. He suggests that oldest regions of the zone are narrowest where isolating mechanisms have had more time to become established. Mayr (1942) does not believe this explanation corresponds with the facts presented by Meise, who observed the width of the hybrid zone of *Corvus* is determined by local ecological factors. Further, narrow stretches of intergradation occur in both recent and older parts of the zone. Because in *Quiscalus*, Huntington (1952) observed no reduced viability or fertility in the intermediates, he feels Dobzhansky's explanation is inadequate in principle, and suggests that increased mixing due to migration, and selective forces favouring the intermediate in a rapidly changing environment are the two main factors affecting the width of area of intergradation.

Because the width of intergradation zones is determined largely by isolating mechanisms, it is appropriate to discuss variation in the width of the tiger beetle hybrid zone in the light of two sets of theories on the origin of isolating mechanisms.

For several hypotheses natural selection is believed to be responsible for the promotion of isolating mechanisms. One representative hypothesis postulates that intermediates are of lowered fertility or viability compared to parental forms. From this it is argued that individuals which enter into mixed pairs will eventually be eliminated from both populations because the hybrids they produce are being selected against. In time, as isolating mechanisms are perfected, the zone of intergradation is contracted. This is essentially Dobzhansky's view.

A second hypothesis treats the origin of isolating mechanisms as an incidental by-product of genetic divergence in isolated populations (Muller, 1940) rather than as the direct result of selection for reproductive isolation. Mayr (1963) points out that many isolating mechanisms vary geographically.

Because many isolating mechanisms have ecological components, any changes in incipient species are certain to affect their isolating mechanisms. The narrowness of the zone in western Alberta can be

due in part to different habitat preferences (see p. 157). Clay, or mud, or sand with organic material, seem to be preferred by *duodecimguttata*, while soils of pure sand or clean gravel are typical *oregona* habitat. In the north, where the intergradation zone is wider, both species may be more broadly adapted. The broader northern zone may also be an effect of better adaptation of intermediates to the northern environment than to that of the south. However, in order to understand this zone of intergradation more completely, ecological investigations should be undertaken.

　　　　The elytral pattern of *duodecimguttata* is complete in western parts of the species range but it is reduced in eastern and southern regions. The full pattern also appear in the zone of intergradation. Eastern *duodecimguttata* specimens often have *oregona* - like elytral markings (see p. 102). This situation may be interpreted as sympatric character divergence, which may be described as follows. Two closely related species of animals overlap geographically. Their differences are emphasized in areas of sympatry so that both species are easily recognized. In ranges where one of the species occurs alone it closely resembles the other species.

　　　　For several reasons it is doubtful that the variation in the elytral pattern of *duodecimguttata* is evidence of character displacement. Some workers observe that character displacement occurs within regions of overlap (Brown and Wilson 1956, Mayr 1963). The complete elytral pattern of *duodecimguttata* is present in the hybrid belt in western Alberta but it is also characteristic of populations far beyond the zone of overlap (fig. 17). In addition variation in elytral pattern of *duodecimguttata* is not complemented by similar clines of other characters. For example the shape of the median lobe of the male is uniform throughout the range of *duodecimguttata* except in the hybrid zone where there are many intermediate shapes ranging from that of *oregona* to that of *duodecimguttata* (see p. 97). Similarly, hairs are present on the frons, top of the head, and post genae of *duodecimguttata* throughout the species range except in the area of intergradation. Furthermore, since there is random interspecific mating in the zone of hybridization, the difference in markings does not serve as an isolating mechanism.

PHYLOGENY AND ZOOGEOGRAPHY OF THE NORTH AMERICAN

SPECIES OF THE *MARITIMA* GROUP

Phylogeny

　　　　The ancestral form of the North American species of the *maritima* group is necessarily reconstructed from features that are widespread among extant species because no fossils are available. The rationale and principles used in re-constructing the characters of a hypothetical ancestor are explained in Cain and Harrison (1960). The characters of the ancestral species were probably as follows: dorsum, brown, opalescent; venter, metallic blue-green; thoracic pleura, copper colored; humeral, apical, and middle lunules, and marginal band, complete;

lunules narrowly expanded as shown by *hirticollis* or *repanda*; shapes of the individual markings like those of *repanda*; hairs present on the head between the eyes; features of the male genitalia as they are now; flanges of the median lobe comparatively narrow like those of *hirticollis* or *repanda*; fields *a*, *b*, and *c* of the internal sac lightly aculeate; sclerites 1, 2, 3, 4, and 6 of the internal sac general size and shape of extent species; sclerite 5 large like those of *hirticollis* and *repanda*; sclerite between 2 and 6 intermediate size between that of *hirticollis* and *oregona*; pronotum of the larva densely pilose. The species was a riparian form, and it gave rise to three lineages (fig. 45).

The first derivative stock (1) was perhaps characterized by an alteration of the elytral pattern in which the posterior portion of the humeral lunule was produced obliquely towards the median line; within the male's internal sac, field *a* and sclerites probably became respectively densely aculeate and considerably reduced; the pronotum of third instar larvae was probably quite pilose.

This primary stock ultimately gave rise to the species *limbata*, *bellissima*, *theatina*, and *columbica*. The species *limbata* and *bellissima* appear to be most closely allied. The subspecies *limbata hyperborea*, and *bellissima* each have the posterior tip of the humeral lunule extending almost to the middle band; sclerite 5 of the male internal sac has been lost in these species; the riparian habit was abandoned and both species are sand dune inhabitants. Beside the differences in shape of their median lobes, *limbata* is very hairy between the eyes and *bellissima* is less so. In this respect, *bellissima* has departed further from the ancestral stock than has *limbata* The southern races of the latter species, however, have lost almost all of the dark pigment of the elytra.

The species *theatina* and *columbica* appear to be more closely related to each other than they are to the other two. A humeral lunule whose posterior tip is briefly extended is a diagnostic feature of *theatina* and *columbica*; a very large triangular sclerite has evolved between 2 and 6 of the male internal sac, and sclerite 5 has not completely disappeared. They differ mainly in two characters: *theatina* is densely hairy between the eyes and lives on sand dunes, while *columbica* is sparsely hairy between the eyes and has retained the riparian ancestral characteristic.

The proposed course for *limbata*, *bellissima*, *theatina*, and *columbica* is not presented in a dichotomous scheme in fig. 45 because different arrangements can be devised on the basis of other similarities among the four species. Distribution of hairs on the head, condition of elytral pattern, color, or habitat preferences each could be used to erect a different hypothetical course, but each of these would imply a greater amount of parallelism or convergence than is required in the scheme I have suggested.

The second lineage (2) is represented by the species *hirticollis* which is somewhat remotely allied to the other existing North American species of the *maritima* group. This form evolved: a humeral lunule the posterior tip of which is distinctly hook-shaped; a comparatively pronounced twirl in sclerite 4, and a very large sclerite between 2 and 6 of the male internal sac; and it has retained a densely pilose pronotum of the third instar larva.

The third ancestral stock (3) probably developed or retained a c-shaped humeral lunule; field *a* of the male internal sac remained lightly

aculeate and sclerite 5 increased in size. Secondary setae probably sparse-
ly covered the pronotum of the third instar larva; and the species was most
likely riparian.   This ancestral stock gave rise to the species *repanda*,
depressula, *oregona*, and *duodecimguttata*.

The species *repanda* appears to be less closely related to the other
three species than they are to one another. Within the male internal sac,
sclerite 5 has become very well developed and the sclerite between 2 and
6 has been lost; *repanda* ranges across North America but no introgression
is evident with the other three species in areas of sympatry.

Evolving from a *repanda* like ancestor, the stock which gave rise to
depressula developed a median lobe with broad flanges, lost most of the frontal
hairs, and developed a modified pattern of white elytral markings, which
at first were extensive but subsequently became much reduced. Also the
ancestral brown color of the dorsum was replaced by blue and green in
the stock which developed reduced markings, and in the east the lowlands
were abandoned by this form for life high in the mountains. Simultaneously
the larva of this derivative form lost most of the pronotal hairs charact-
eristic of the pronotum of the ancestral stock.

Another derivative stock from a *repanda* - like ancestor, was the
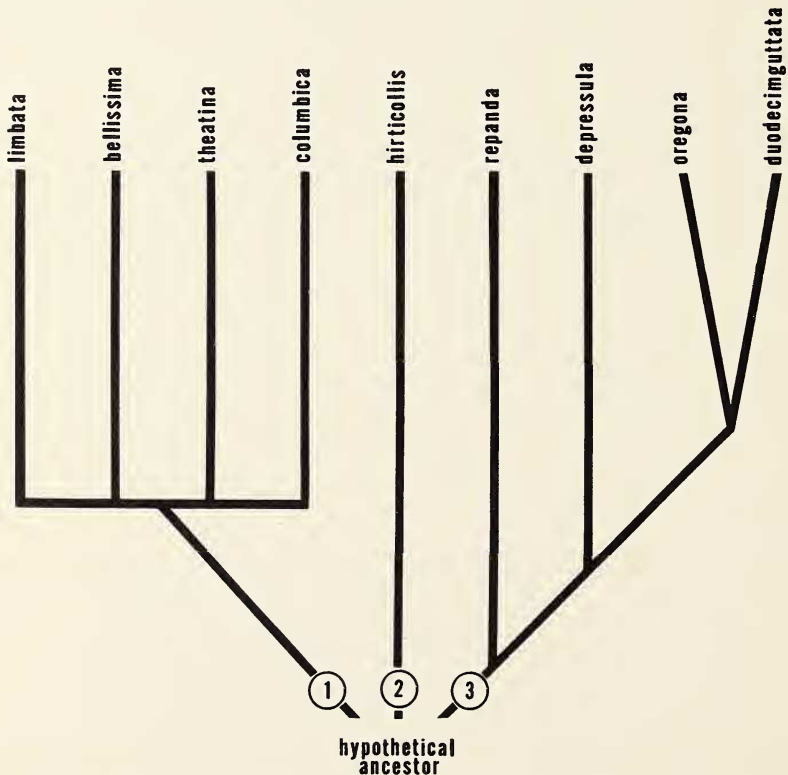
Fig. 45. Hypothetical phylogeny of the North American species of the *martima* group.

progenitor of *duodecimguttata* and *oregona*. This stock developed at first slightly reduced elytral markings. Subsequently it became divided into two geographically isolated groups the western of which lost the frontal hairs, developed strongly reduced elytral markings, and throughout much of its range the brown color of the dorsum was replaced by green, blue, or purple, and the pleural sclerites became blue or green. The pronotum of the larva gradually lost much of the pubescence evident in the ancestral larva. This western isolate is the species *oregona*. In the eastern isolate, the elytral markings were also reduced, and blue and green color of the dorsum appeared. The mutations producing reduced markings became widespread replacing the ancestral condition throughout most of the range of the species. Hairs on the pronotum of the larva were reduced in number. This eastern isolate is the species *duodecimguttata*. Following a period of separation too short to permit the development of complete reproductive isolation the eastern and western stocks met one another and a narrow zone of hybridization developed in the area of contact.

This scheme requires postulation of an appreciable amount of parallel evolution. Frontal hairs were lost or reduced four times. Green or blue color of the dorsum was developed six times. Broad flanges on the median lobe were developed six times. The primitive elytral pattern was lost five times, but by two different phyletic branches. In one of these extensive reduction of lateral pigmentation took place. The other type of pattern breakdown was developed by increased pigmentation.

Thus these species, together form a structurally uniform group in which a number of similar structures have arisen independently. This suggests that the group possesses a good degree of evolutionary homodynamy (Bock 1963). This principle is defined as follows: "The number of times and ease with which an identical or very similar feature may arise independently within a group depends upon its degree of evolutionary homodynamy which in turn depends upon its common genetical-developmental potential." In the light of this principle similar structures that have arisen independently in the North American *maritima* group are considered to be homologous in the broad sense, which is defined by Bock as follows: "homologous features (or conditions of the features) in two or more organisms are ones that can be traced back to the same feature (or condition) in a group possessing a high degree of evolutionary homodynamy."

Zoogeography

The following account of the development of the distribution of the North American species of the *maritima* group is hypothetical. Movements, and times and place of origin of extant species are necessarily constructed on the basis of: distribution and morphological features of the species, geological and climatic events of the Tertiary and Pleistocene in North America, and rates of evolution in some other groups of insects.

Insects generally develop modifications of structural features at a slow rate. Many fossil species of the early or middle Tertiary closely resemble existing species (Linsley 1958, Ross 1958, Becker 1963, Quate 1963, Sabrosky 1963, and Sturtevant 1963). Most of these are members of recent genera. However, Zeuner (Sylvester - Bradley, 1963), by means of analysis of 212 species of fossil Apoidea, Lepidoptera,

and Saltatoria,   reckons that excepting the honey-bee all living species evolved in the Pleistocene. He estimates half to one million years is a reasonable time required for the evolution of a full species. Zeuner further notes that no insect species are known with certainty to have survived from the Miocene (see Zeuner 1943, for more information of the time factor in evolution of insects). There is no evidence of recent vigorous evolution within the North American species of the *maritima* group. Indeed these are rather primitive in comparison with other species groups of   *Cicindela*.   The ancestral stock of the *maritima* group may have been in existence during the early Tertiary. Living species may have evolved during the later Tertiary or early Pleistocene.

Historical events which may have effected geographical isolation and subsequent speciation of tiger beetle populations are of importance. Thus it is necessary to review briefly geological and climatic changes in western North America during the Tertiary and Pleistocene (see Blackwelder 1948, King 1958, MacGinitie 1958, Martin 1958, and Mengel 1964).

The Tertiary was marked by several periods of crustal dis- turbances.   Early Tertiary was a time of extensive mountain building through the west, and it was then the initial Rocky Mountain system was thrust up. Crustal folding was renewed in the middle Tertiary (late Miocene). Gentle folding in the Rockies prevailed. Disturbances were evident in coastal and southeastern California, and southern Nevada, while other mountains were widely distributed throughout the American west. A chain of volcanoes was built up along the east flank of the Sierra Nevada and Cascade Mountains. Large basins were produced, many of which became lake basins. At the close of the Tertiary (late Pliocene)once again crustal folding occurred along the Pacific coast, and in Nevada and Utah. The modern California Coast Range, Wasatch and Ruby Mountains and many others were elevated during this period. The southwestern plateau was raised to its present level, and most of the interior drainage systems were renewed.

Early Miocene and most of the Pliocene were periods of relative quiet. Stream systems wore down western mountains to scattered hills, and extensive plains were formed on which large lakes drained or w e r e filled.

The climate in the early Tertiary was warmer than now. Tropical forests filtered into the north Temperate Zone while temperate conditions prevailed in Rocky Mountain regions. In the Miocene the climate became cooler and temperatures steadily decreased into the Pleistocene. Simultaneously climatic zones moved southward and southwestern regions became drier.

The end of the Tertiary and beginning of the Pleistocene was characterized by the gradual development of mountain glaciers and con- tinental ice masses. There were five major glacial stages in North America, the Nebraskan, Kansan, Illinoian, Iowan, and Wisconsin. Between these occurred long warm periods, the Aftonian, Yarmouth, Sangamon, and Prairie.

In glacial periods glaciers extended southward along mountain ranges.   These gave rise to rivers which descended onto open basins where much sand and glacial till was deposited. Large lakes developed

in nearly all western basins.

Climate and vegetation similar to those of the present time were prevalent in interglacial periods in northern latitudes.

All of the North American species of the *maritima* group live in subarctic to warm temperate regions. Perhaps the ranges of *hirticollis* and *oregona* extend for a short distance into Mexico but for the most part they are northern forms. The species, *hirticollis* and *repanda* are almost transcontinental and inhabit regions from the Cascades in the west to the Atlantic coast. Ranging from the Atlantic seaboard to the eastern slopes of the Rockies *duodecimguttata* is the only true eastern form. Inhabiting areas from the Rocky Mountains to the Pacific coast *oregona* is the western counterpart of *duodecimguttata*. The species *depressula* is restricted to high elevations of the Cascade Range and Sierra Nevada, and in river valleys near the Pacific coast from northern California to southern Alaska. The species *limbata* inhabits areas just east of the Continental Divide. Further south, however, populations are found in Kane County, Utah (*l. albissima* Rumpp). The ranges occupied by *bellissima*, *theatina*, and *columbica* are rather restricted:San Luis Valley in south-central Colorado, is the entire range of *theatina*; *bellissima* occurs on sea beaches in western Oregon and southwestern Washington;while *columbica* exists in southeastern Washington on beaches of the Snake River.

Knowledge of the distribution of the North American species of the *maritima* group supports the premises that: the ancestral species was a cool adapted form, and mountain ranges of western North America are effective geographical barriers particularly the Rocky Mountain system.

The relationships of the Nearctic species of the *maritima* group to those of the Old World members are not understood (but see Papp 1952), so speculation on time and direction of intercontinental movements is not warranted. However it seems certain that such movements did occur, probably by way of a Bering land bridge (see Gressitt 1963). The hypothesis which follows is based on the as yet unestablished premise that all the Nearctic species are more closely related to one another than to any Palearctic species.

The primitive ancestor of the North American species of the *maritima* group may have inhabited cool - temperate: regions of North America in late Miocene. By virtue of its habits it may have filtered southward along alpine river systems near revived mountains of western North America. It may have assumed a reticular distribution among these mountains and in cooler regions further east. By the continuous folding of strata, and volcanic eruptions, populations probably became disjunct and geographically isolated. The first three derivative stocks may have been established during the course of this unsettled period.

Very little can be said about the place of origin and geographical movements of *hirticollis* because of its present vast range and widespread sympatry with *repanda, oregona,* and *duodecimguttata.* It is probably a relatively old form.

The derivative stock that gave rise to *limbata, bellissima, columbica,* and *theatina* , may have ranged throughout cooler regions of western North America up to the late Pliocene. Western North America had been worn down to extensive plains. Mountains were no longer effective geographic barriers, and sandy habitats occurred abundantly near the coast, near

lakes and rivers, and in dry areas remote from water. Perhaps during its existance the ancestral species became more generally adapted and improvements of functions allowed it to inhabit sandy environments in arid regions, but it also continued its riparian habits. The renewed crustal unrest of the later Pliocene probably disbanded and isolated populations, that evolved into *limbata, bellissima,* and *theatina.*

The species *limbata* may have developed as a sand dune inhabitant on the northeastern side of the revived Rocky Mountains in late Pliocene or early Pleistocene. The original form probably resembled the boreal subspecies *l. hyperborea.* Southern populations were probably established during cooler glacial periods. See Rumpp (1961), for some ecology and mechanism of lost of elytral pigmentation in southern populations of *limbata.*

The ancestral stock of *bellissima,* probably became isolated on the Pacific coast by the renewed folding of the Coast Range in late Pliocene or early Pleistocene.

Populations that evolved into *columbica* probably became locked in by the Sierra Nevada and Rocky Mountains perhaps in the early Pleistocene. Within this area they retained the riparian habits of the ancestral stock.

The species *theatina* may have originally been isolated from other related populations to the east of the Continental Divide in Colorado. It perhaps had a greater range than the San Luis Valley to which it is now restricted.

The ancestral stock from which *repanda, depressula, oregona,* and *duodecimguttata* evolved may have originally been isolated to the east of the Rockies. It eventually became transcontinental, probably in early Pliocene.

The place and time of origin, and subsequent geographical distribution of *repanda* is obscured because it ranges throughout most of temperate North America and is sympatric with several related species, and perhaps speciated before late Pliocene.

The species *depressula* may have developed in late Pliocene. Primitive populations of *depressula,* represented by *d. eureka,* on the west side of the Cascade Range and northern Sierra Nevada probably became geographically segregated from the form which gave rise to *duodecimguttata* and *oregona.*

The common ancestor of the species *duodecimguttata* and *oregona* probably occupied the entire cool temperate North America during the middle Pleistocene. The extant species may have been formed during the middle Pleistocene. Dissection of the range of the ancestral stock took place in glacial periods of the later Pleistocene when ice masses covered Canada and glaciers spread southward on high mountain ranges. The species *duodecimguttata* evolved in the east and *oregona* in the west with the Rockies acting as the major geographical barrier. In glacial periods it is doubtful that populations of *duodecimguttata* merged with those of *oregona* in southeastern regions of the Rockies for no evidence of that exists. Hybridization between these species is proof of their close relationship and that their reproductive isolating mechanisms have not yet become fully developed. Perhaps hybridization between them was more extensive in earlier interglacial periods and their isolating mechanisms have become gradually more effective with each successive glacial period.

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